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ENGLAND.

AGE CHANGES AND VARIABILITY IN THE SKULLS AND TEETH OF THE CENTRAL AMERICAN MONKEYS *ALOUATTA*, *CEBUS* AND *ATELES*

BY

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[Accepted 9th December 1958]

(With 3 plates and 7 figures in the text)

CONTENTS

	Page
Introduction	337
Material and methods	338
Absolute size of cranial measurements of adults	343
Cranial indices and form of forehead of adults	354
Age changes in cranial measurements	361
Sutures and fontanellar bones	372
Variations in some special cranial features	376
Age changes in dentition	378
Abnormal and diseased conditions of the skull and teeth	380
Summary	385
References	389

INTRODUCTION

In 1923 the author, while working on human foetal growth and variability in the Laboratory of Embryology of the Carnegie Institution of Washington, had spent his vacation in eastern Nicaragua for the purpose of collecting comparative material of monkeys. A second trip to the same place in the summer of 1924, sponsored by the just named institution, resulted in collections which have been very helpful for many investigations by various authors and which supported in at least a preliminary way the conclusion that monkeys of one and the same kind, living in a strictly uniform environment, can vary individually fully as much as modern man (Schultz, 1926). In 1929 and again in 1932 the author was enabled to participate in two field trips to Chiriqui in western Panama which had been organized by Dr Herbert C. Clark, then Director of the Gorgas Memorial Laboratory of Tropical Medicine, for a survey of wild monkeys as possible carriers of malaria. The very considerable series of monkeys obtained on the latter two trips in the immediate neighbourhood of only two closely adjacent camps, were shot primarily for the examination of their blood by Dr Clark and the collection of parasites of all kinds by the late Professor R. Hegner, but were utilized also for the preservation of comparative-anatomical material by the late Professor G. B. Wislocki and for the intensive study in the field of age changes and of variability in all fresh bodies as well as for the collection of at least the skulls by the author. In these four trips there have been brought together 379 skulls of howler monkeys, capuchin monkeys and spider monkeys (besides marmosets and night monkeys, not used here), which form a part of the author's primate collections and thus could all be measured again for the present investigation.

Between 1949 and 1951 Dr H. Clark and his staff as well as the Panama Health Department, in connection with a survey of possible carriers of yellow fever, collected again samples of the monkey population of Panama and of southern Mexico and later on presented the large series of skulls, obtained on these trips, together with exact records on locality, sex, weight and autopsy findings, to the U.S. National Museum in Washington, D.C. Doctor Clark very kindly suggested to the writer that he should study this new material which is directly comparable to and, indeed, partly from the identical localities as the author's own Panamanian collection. In 1956 it became possible to make use of this unique opportunity with the aid of a generous grant from the Wenner-Gren Foundation for Anthropological Research. To the president, Dr P. Fejos, and to the board of directors of this foundation the writer expresses his profound gratitude for their interest in and support of this investigation. To the director of the U.S. National Museum, Dr R. Kellogg, and to the curator of the Division of Mammals in this great museum, Dr D. H. Johnson, the writer is very grateful for their permission to study not only the new material of Dr Clark, but also all their other skulls of corresponding Central American species. The 532 skulls examined at the National Museum, added to the 379 skulls in the author's collection form the rare total of 911 specimens which permits a detailed statistical analysis of cranial variability in general, of sexual differentiation, of possible tendencies for race formation and of postnatal changes with age in skulls and dentitions. In addition this extensive material can give a fairly representative indication of the variety and frequency of pathological and teratological conditions among these wild primates and this not only according to species, but also in the different age groups and in the two sexes. It is specially mentioned that all this material had been examined in the field by very competent and reliable collectors so that the sex of even the youngest specimens is known with certainty.

Some taxonomists may disagree with the writer's conviction that each of the three genera, to be dealt with here, is represented in Central America by only one species which here or there possibly differs locally enough to have formed some geographic races or sub-species. In the writer's experience none of the cranial and dental characters differ between any of the local series to such a degree that the corresponding ranges of variations do not overlap very extensively. To justify any separation into species by possible differences in the colour or other features of the hair alone seems most hazardous whenever the skulls show no constant differences. The author, however, does not aim to enter into any taxonomic controversies. The main purpose of this paper is the contribution of new exact data on the variability and the age changes in wild New World monkeys for ultimate comparison with the corresponding findings in Old World primates, particularly man.

MATERIAL AND METHODS

The material to be discussed here consists of the following three species : *Alouatta palliata* (Gray), *Cebus capucinus* (Linnaeus) and *Ateles geoffroyi* (Kuhl). All are wild-shot specimens from localities ranging between the Panama Canal Zone and southern Mexico. As will be shown, a few minor

geographic differences within these species do exist, but a subspecific separation seems fully adequate in all instances, a view expressed also by most of the modern taxonomists who have dealt with these primates. For instance, Lawrence (1933) recognizes seven subspecies of *Alouatta palliata*, but states that " subspecific variation amongst these monkeys is notably very small and individual variation is relatively great. . . in most cases extreme individuals may be found in each group that resemble very closely individuals of some other subspecies ". For *Cebus capucinus* Hershkovitz (1949) retains tentatively the names of five subspecies, but adds that " none of the distinguishing characters attributed to the described races of *C. capucinus* appears to be valid ". Kellogg & Goldman (1944) have listed nine subspecies of *Ateles geoffroyi* which seem to differ almost exclusively in regard to their skins, and it is specially mentioned that " all the races of *A. geoffroyi* agree closely in the more important cranial details, but in the more northern subspecies *vellerosus* and *yucatanensis* the brain case is slightly narrower than in *panamensis* and other Middle American races ". Since all these races can at best be distinguished only with the aid of skins, which had not been saved in a great many of the specimens discussed here, the present material has been grouped according to the countries of origin and thus will be simply referred to as " Nicaraguan series ", " Mexican series ", etc. Table 1 shows the distribution of all available material according to country, age and sex. It is specially to be mentioned that *all* of the howling monkeys and spider monkeys in the Nicaraguan series had been collected by the author in one very limited region in the Princapolka river valley and should, therefore, represent a very homogeneous population sample. The great majority of the Panamanian spider monkeys are from the westernmost part of the province of Chiriqui, but all the other geographic series are composed of specimens from more or less scattered localities within the respective countries. The comparatively few specimens from Costa Rica, Honduras and Guatemala have here been included merely to find out whether or not they differ significantly from the other local races of the respective three species. For the latter, small local series it would not have been justified to record here their standard deviations and other statistical data besides the ranges of variations and averages and, indeed, not even the latter have been specially tabulated for the few skulls of *Cebus* from Honduras, though they have been used in connection with non-metric analyses. In all subsequent tables the data are based upon exactly the same numbers of specimens as are listed in Table 1. The very few and minor exceptions were caused by the loss of incisors *intra vitam*, preventing the determination of the type of occlusion and by the destruction of the infraorbital region by shot or by infection, leaving the number of infraorbital foramina too uncertain for counting in a few instances.

Since the series listed in Table 1 are unusually large in their totality a few remarks seem justified here regarding the composition of this material according to age and sex. As shown by Table 2, from 19 to 29 per cent of all the skulls are those of immature specimens and only between 5 and 8 per cent of all skulls are those of evidently old animals with teeth extremely worn and at least beginning signs of senile bony atrophy. When it is considered that the great majority of these specimens had been collected by Dr Clark and by the

author for purposes which made the immature fully as desirable as the adult specimens, it does seem surprising that the young animals do not form a larger part of these population samples. In his census of the living howlers on Barro Colorado Island (Panama C.Z.) of 1933 Carpenter (1934) counted

TABLE 1

Distribution of the entire material according to species, country, age and sex. The adults are separated in three classes of advancing dental wear, **0** indicating the youngest and **2** the oldest of all adults.

Species	Age	Sex	Panama	Costa Rica	Nicaragua	Honduras	Guatemala	Mexico	Total
Alouatta palliata	infantile	♀	9	–	5	–	–	2	16
		♂	8	–	2	–	–	1	11
	juvenile	♀	25	1	24	–	–	3	53
		♂	22	–	9	–	1	3	35
	adult 0	♀	51	2	16	–	3	11	83
		♂	18	3	10	–	5	4	40
	adult 1	♀	80	5	40	–	6	7	138
		♂	32	3	34	–	7	5	81
	adult 2	♀	13	–	4	–	–	3	20
		♂	7	1	6	–	1	1	16
	Total	♀ & ♂	265	15	150	0	23	40	493
Cebus capucinus	infantile	♀	5	–	3	–	–	–	8
		♂	5	–	–	–	–	–	5
	juvenile	♀	14	–	–	1	–	–	15
		♂	17	–	4	–	–	–	21
	adult 0	♀	15	–	4	–	–	–	19
		♂	22	–	7	1	–	–	30
	adult 1	♀	26	–	7	1	–	–	34
		♂	24	–	2	1	–	–	27
	adult 2	♀	4	–	1	–	–	–	5
		♂	3	–	–	–	–	–	3
	Total	♀ & ♂	135	0	28	4	0	0	167
Ateles geoffroyi	infantile	♀	1	–	1	–	–	3	5
		♂	2	–	–	–	–	2	4
	juvenile	♀	10	–	6	–	–	1	17
		♂	12	–	2	–	–	8	22
	adult 0	♀	26	1	9	–	1	10	47
		♂	11	–	5	–	2	7	25
	adult 1	♀	34	5	13	–	2	14	68
		♂	16	4	6	–	1	15	42
	adult 2	♀	3	1	3	–	–	4	11
		♂	3	–	3	–	–	4	10
	Total	♀ & ♂	118	11	48	0	6	68	251

215 young and 274 adult monkeys, the former amounting to 44 per cent of the entire population. In a census of living spider monkeys by Carpenter (1935), made while he was with Dr Clark and the author in Chiriqui (Panama), the immature specimens formed 33 per cent of the total population of 181 observed monkeys. Though his percentage is also much lower than that for the howlers, it is again much higher than the corresponding figure in Table 2 and a more detailed analysis of the figures of Carpenter and those in Table 1 shows the greatest discrepancy in the infantile age groups. From the same two detailed reports by Carpenter one can obtain the sex-ratios of living adults as 43 for howlers (census 1933) and as 61 for spider monkeys. The latter figure is exactly the same as that for the skulls of *Ateles*, but the former figure is even lower than the ratio for skulls of adult *Alouatta*. It appears safe to conclude that among adult howler monkeys there are somewhere near twice as many females as males and that in adult spider monkeys there is also a very marked preponderance of females, but in capuchin monkeys both sexes are about

TABLE 2

Percentage participation of the different age groups in the total series and sex ratios (x ♂ : 100 ♀) of different age groups, based upon the data in Table 1.

	Age group	Alouatta	Cebus	Ateles
per cent of total population sample (♀ + ♂)	immature (inf. + juv.)	24	29	19
	mature (ad.o)	25	29	29
	middle-aged (ad.1)	44	37	44
	old (ad.2)	7	5	8
Sex ratio	immature	67	113	118
	all adults	57	103	61

equally represented among adults, perhaps in some connection with the fact that these monkeys do not congregate in as large groups as the other two species, at least according to the author's observations. In all three species the sex ratio decreases in general with age, indicating a greater mortality in males than in females, most marked among spider monkeys.

In order to be able to make some preliminary comparisons regarding age changes and sex differences with at least one ape and man the author has measured also the following series of skulls: 17 infants and 50 adults of chimpanzee and 14 infants and 42 adults of man, all from the collections in the

anthropological institute at Zürich. Since the chimpanzee material contains representatives of various races the human series have also been mixed, containing 12 Whites, 20 Negroes and 24 old Egyptians, but for each infantile skull of one race and sex three adult skulls of the same race and sex have been selected.

All the skulls have been assigned to the following age groups, based upon the condition of the dentition :

Infantile = specimens with at least some and at most all deciduous teeth.

Juvenile I = specimens with one to four first permanent molars and such middle permanent incisors as occasionally appear before the upper M 1 have fully erupted.

Juvenile II = specimens which possess more permanent teeth than in the juvenile I stage, but without having the last permanent teeth (M 3 and/or C) fully erupted.

Adult **0** = specimens with completed second dentition, but as yet without noteworthy wear of the teeth.

Adult **1** = specimens with moderate to marked wear of the teeth (" middle-aged adults ")*

Adult **2** = specimens with very marked to extreme wear of the teeth and cranial indications of old age.

The following seventeen measurements (in mm.) have been taken on all skulls in a strictly uniform manner :

1. Length = midsagittal point of naso-frontal suture (*Nasion*) to most distant midsagittal point on occiput, disregarding possible occipital crests or processes.
2. Breadth = greatest breadth of braincase perpendicular to midsagittal plane above the roots of the zygomatic arches on temporal squamae or parietals.
3. Height = from midsagittal point on oral border of foramen magnum (*Basion*) to vertex perpendicular to lower surface of basi-occipital, disregarding possible sagittal crests.
4. Basal length = *basion* to *nasion*.
5. *Basion-prosthion* length = *basion* to lowest point on alveolar border between the upper middle incisors (*Prosthion*).
6. *Nasion-prosthion* height = straight distance between these two points.
7. Bizygomatic breadth = greatest breadth between the zygomatic arches.
8. Biorbital breadth = greatest breadth between the lateral walls of the orbits above the level of the lower orbital border.
9. Postorbital breadth = smallest breadth of the postorbital constriction.
10. Interorbital breadth = smallest breadth between the medial walls of the orbits at the orbital rims.
11. Orbital height = greatest perpendicular diameter of the orbital entrance.
12. Palatine length = from *prosthion* to middle of a tangent on the most aboral points of the r. and l. alveolar processes.
13. Palatine breadth = greatest breadth between the outer alveolar borders of the teeth behind the canines.
14. Postcanine length = greatest straight distance between the crowns of the upper teeth of one side behind the canine.

* The adults of this age group had really been separated into those with *moderate* and those with *marked* dental wear, as had been done in the author's (1958) similar study on *Colobus* skulls. Such a distinction, however, seems particularly difficult in these platyrrhines, so that finally all those skulls which showed neither lack of wear nor extreme wear were assigned to a single group " **1** ".

15. Canine thickness = greatest sagittal diameter of the neck of one upper canine or, if both are lost, of one corresponding alveolus.

16. Mandibular length = from oral alveolar border between the lower middle incisors to the middle of a tangent on the mandibular condyles.

17. Distance between temporal lines = smallest straight distance between the r. and l. temporal lines.

In addition to the above measurements the numbers of infraorbital and of mental foramina were recorded for each skull, as also the stage of closure of the main sutures and the degree of fusion between the mandibular halves and between the occipital elements. Further records were made of dental eruption or attrition, occlusion and of all anomalies and pathological conditions.

ABSOLUTE SIZE OF CRANIAL MEASUREMENTS OF ADULTS

The ranges of variations and averages of all the seventeen cranial measurements in adults are listed in the accompanying tables according to species, country and sex. For seven of the more important measurements the standard deviations, variation coefficients and probable errors are also given for the series which are sufficiently large to warrant these calculations.

The Tables 3 to 6 contain the data for *Alouatta palliata*. From comparisons of these data it is apparent that the ranges of variations in all the geographic series overlap extensively and often even completely, even though the averages can at times differ appreciably. In regard to the length, breadth and height of the brainpart of the skull the corresponding averages differ among all five local series for never more than 3 mm. In the basal length the greatest average difference is 5·1 mm. and in the postorbital breadth 1·8 mm. Most of the average dimensions of the face-part of the skull also differ among all series for at most only very few millimetres, but the basion-prosthion length and the mandibular length show quite marked differences in size between the Panamanian and the Guatemalan and Mexican series. The latter differences indicate that the face can project forward in varying degrees in some local representatives of *Alouatta palliata*. It is of interest to note that the series with the most marked prognathism (indicated by the greatest basion-prosthion length and mandibular length) are not also distinguished by exceptionally great palatine and postcanine lengths. The Guatemalan and Mexican howlers also show the greatest average interorbital breadth, but the ranges of this measurement overlap with the corresponding ranges in the other series.

The howlers from Coiba island, off the pacific coast of Panama, have been regarded as a distinct species, *Alouatta coibensis* Thomas, by e.g. Goldman (1920) on account of their small size. Actually, however, there occur just as small or even smaller individuals among the howlers from the mainland of Panama, as shown by the data in Table 6. In this instance, as in all other geographic series, the metric differences in the skulls of adult howlers from Central America are certainly nowhere any more marked than differences in corresponding cranial measurements among the races of *Homo sapiens*.

The absolute size of the cranial dimensions of adult *Cebus capucinus* differs little between those from Panama and those from Nicaragua, as shown by the data in the Tables 7 and 8. The few available specimens from Honduras all

TABLE 3

Ranges of variations, averages, standard deviations, variation coefficients and their probable errors for seven cranial dimensions of adult *Alouatta palliata*. The numbers of specimens in these series are the same as given in Table 1.

Measurement	Series	Females				Males			
		Range	A ± E (A)	σ ± E (σ)	C ± E (C)	Range	A ± E (A)	σ ± E (σ)	C ± E (C)
Length	Panama	62 - 77	69.1 ± 0.17	2.98 ± 0.12	4.31 ± 0.17	65 - 80	73.8 ± 0.31	3.54 ± 0.22	4.80 ± 0.30
	Nicaragua	65 - 73	69.3 ± 0.14	1.64 ± 0.10	2.37 ± 0.15	70 - 81	74.3 ± 0.16	1.64 ± 0.11	2.21 ± 0.15
	Mexico	66 - 73	70.1 ± 0.28	1.93 ± 0.20	2.75 ± 0.29	72 - 82	76.5 ± 0.62	2.88 ± 0.43	3.77 ± 0.57
Breadth	Panama	43 - 53	49.3 ± 0.09	1.65 ± 0.07	3.35 ± 0.13	49 - 57	51.4 ± 0.14	1.59 ± 0.10	3.09 ± 0.19
	Nicaragua	46 - 52	49.7 ± 0.25	1.44 ± 0.09	2.90 ± 0.18	49 - 58	52.1 ± 0.15	1.58 ± 0.11	3.03 ± 0.20
	Mexico	45 - 52	48.8 ± 0.24	1.63 ± 0.17	3.34 ± 0.35	49 - 53	50.7 ± 0.30	1.42 ± 0.21	2.80 ± 0.42
Height	Panama	36 - 42	38.3 ± 0.07	1.28 ± 0.05	3.34 ± 0.13	35 - 42	38.8 ± 0.12	1.35 ± 0.08	3.48 ± 0.22
	Nicaragua	36 - 39	37.6 ± 0.07	0.85 ± 0.05	2.26 ± 0.14	36 - 40	38.0 ± 0.08	0.89 ± 0.06	2.34 ± 0.16
	Mexico	36 - 42	39.2 ± 0.23	1.56 ± 0.16	3.98 ± 0.41	37 - 43	40.1 ± 0.31	1.44 ± 0.22	3.59 ± 0.54
Basal length	Panama	53 - 65	59.4 ± 0.14	2.53 ± 0.10	4.26 ± 0.17	57 - 73	66.0 ± 0.30	3.36 ± 0.21	5.09 ± 0.32
	Nicaragua	56 - 62	58.9 ± 0.11	1.28 ± 0.08	2.17 ± 0.13	61 - 71	65.4 ± 0.18	1.94 ± 0.13	2.97 ± 0.20
	Mexico	57 - 65	61.4 ± 0.34	2.33 ± 0.24	3.80 ± 0.40	66 - 75	70.5 ± 0.58	2.70 ± 0.41	3.83 ± 0.58
Nasion-prosthion	Panama	32 - 43	36.4 ± 0.11	2.01 ± 0.08	5.52 ± 0.22	35 - 48	40.8 ± 0.23	2.61 ± 0.16	6.39 ± 0.40
	Nicaragua	34 - 41	37.0 ± 0.13	1.47 ± 0.09	3.97 ± 0.25	38 - 47	42.1 ± 0.21	2.16 ± 0.14	5.13 ± 0.34
	Mexico	35 - 43	39.3 ± 0.36	2.44 ± 0.25	6.21 ± 0.65	37 - 50	44.5 ± 0.92	4.32 ± 0.65	9.71 ± 1.46
Palatine length	Panama	35 - 44	40.6 ± 0.09	1.63 ± 0.07	4.02 ± 0.16	41 - 49	44.8 ± 0.17	1.97 ± 0.12	4.40 ± 0.28
	Nicaragua	39 - 44	41.3 ± 0.10	1.15 ± 0.07	2.78 ± 0.17	43 - 50	45.7 ± 0.16	1.67 ± 0.11	3.65 ± 0.24
	Mexico	40 - 46	41.8 ± 0.29	1.95 ± 0.20	4.66 ± 0.48	43 - 49	46.5 ± 0.36	1.70 ± 0.26	3.65 ± 0.55
Postcanine length	Panama	25 - 33	30.8 ± 0.07	1.24 ± 0.05	4.03 ± 0.16	31 - 36	32.7 ± 0.11	1.24 ± 0.08	3.79 ± 0.24
	Nicaragua	30 - 33	31.6 ± 0.07	0.81 ± 0.05	2.56 ± 0.16	31 - 36	33.5 ± 0.11	1.21 ± 0.08	3.61 ± 0.24
	Mexico	29 - 34	31.4 ± 0.20	1.34 ± 0.14	4.27 ± 0.44	31 - 35	33.3 ± 0.30	1.42 ± 0.21	4.26 ± 0.64

TABLE 4

Ranges of variations and averages of the same seven cranial dimensions as in Table 3 of the adult *Alouatta palliata* of the two smallest series. For numbers of specimens see Table 1.

Measurement	Series	Females		Males	
		Range	Aver.	Range	Aver.
Length	Costa Rica	68 - 73	70.7	74 - 80	76.7
	Guatemala	68 - 71	69.8	72 - 79	75.5
Breadth	Costa Rica	48 - 52	49.6	52 - 52	52.0
	Guatemala	47 - 54	49.3	48 - 54	50.7
Height	Costa Rica	37 - 40	38.6	38 - 40	39.3
	Guatemala	37 - 40	38.2	38 - 43	40.3
Basal length	Costa Rica	57 - 61	59.1	64 - 67	66.3
	Guatemala	58 - 66	62.8	63 - 75	69.7
Nasion-prosthion	Costa Rica	35 - 36	35.7	39 - 44	42.6
	Guatemala	36 - 44	40.5	36 - 52	45.7
Palatine length	Costa Rica	40 - 43	41.3	44 - 48	46.1
	Guatemala	40 - 45	43.2	44 - 50	47.5
Postcanine length	Costa Rica	30 - 32	31.1	32 - 35	33.4
	Guatemala	30 - 35	33.0	32 - 35	33.9

fall well within the ranges of variations for the two large series. The averages of most the measurements in both sexes are slightly smaller in the Nicaraguan than in the Panamanian series. As among the *Alouatta*, so in these *Cebus* the most marked difference exists in the basion-prosthion distance, according to which the capuchin monkeys from Nicaragua tend to be somewhat less prognathous than those from Panama.

The five geographical series of *Ateles geoffroyi* also show few consistent and really significant differences in the size of the cranial dimensions, as is evident from the data in the Tables 9 to 11. Some of the average values do differ according to locality, but the probable errors of these averages, as well as the corresponding ranges of variations, demonstrate that such *average* differences are merely due to locally varying trends to produce fewer or more large individuals, respectively such which are slightly differing in one or another single dimension. Again it must be concluded that these tables contain no data in support of the recognition of separate species of *Ateles* in Central America.

TABLE 5

Ranges of variations and averages of ten additional measurements of the same adult *Alouatta palliata* as in the Tables 3 and 4.

Measurement	Series	Females		Males		Measurement	Series	Females		Males	
		Range	Aver.	Range	Aver.			Range	Aver	Range	Aver.
Basion - prosthion	Panama	72 - 90	81.1	78 - 101	92.1	Orbital height	Panama	19 - 25	21.5	20 - 24	22.3
	Costa Rica	78 - 82	80.7	89 - 98	94.6		Costa Rica	21 - 22	21.6	21 - 23	22.1
	Nicaragua	76 - 86	81.2	88 - 99	93.6		Nicaragua	20 - 23	21.3	20 - 24	22.3
	Guatemala	79 - 96	89.3	89 - 114	103.5		Guatemala	20 - 24	21.8	21 - 25	22.5
	Mexico	79 - 96	87.0	92 - 114	103.5		Mexico	20 - 24	21.8	22 - 25	23.1
Bizygomatic breadth	Panama	62 - 82	70.5	69 - 89	80.7	Palatine breadth	Panama	32 - 40	37.1	37 - 43	40.1
	Costa Rica	67 - 77	71.3	77 - 86	82.4		Costa Rica	36 - 40	37.8	40 - 42	41.1
	Nicaragua	62 - 73	70.1	76 - 90	82.0		Nicaragua	35 - 39	37.6	39 - 44	41.2
	Guatemala	67 - 73	69.9	73 - 86	80.8		Guatemala	36 - 41	38.2	38 - 45	42.0
	Mexico	62 - 73	69.1	78 - 86	81.8		Mexico	35 - 41	37.6	39 - 44	41.9
Biorbital breadth	Panama	50 - 68	58.4	57 - 74	66.4	Canine thickness	Panama	5 - 8	6.0	7 - 10	8.1
	Costa Rica	59 - 63	60.6	66 - 71	69.4		Costa Rica	6 - 7	6.1	7.5 - 8.5	7.8
	Nicaragua	55 - 64	60.7	65 - 77	71.0		Nicaragua	5 - 7	5.9	7 - 9	7.8
	Guatemala	57 - 63	58.9	59 - 72	66.1		Guatemala	5.5 - 7	6.2	7.5 - 9	8.5
	Mexico	50 - 63	58.8	60 - 74	67.5		Mexico	5.5 - 7	6.2	8 - 9	8.2
Postorbital breadth	Panama	36 - 43	40.0	38 - 44	40.7	Mandibular length	Panama	66 - 85	75.1	72 - 94	85.2
	Costa Rica	37 - 42	39.6	40 - 47	41.6		Costa Rica	74 - 79	76.4	81 - 92	87.7
	Nicaragua	37 - 43	40.1	39 - 43	40.9		Nicaragua	70 - 79	75.7	83 - 94	87.6
	Guatemala	37 - 42	39.8	36 - 45	39.8		Guatemala	74 - 86	79.8	85 - 104	93.8
	Mexico	38 - 43	40.2	37 - 42	40.3		Mexico	70 - 85	78.5	83 - 102	92.9
Interorbital breadth	Panama	7 - 12	9.6	9 - 15	11.3	Distance b. tempor.lin.	Panama	6 - 28	17.5	1 - 25	10.1
	Costa Rica	8 - 11	9.4	9 - 13	11.4		Costa Rica	13 - 20	16.6	2 - 22	8.6
	Nicaragua	7.5 - 11	9.2	9 - 13	11.3		Nicaragua	12 - 28	18.2	2 - 22	9.4
	Guatemala	8.5 - 13	10.8	11 - 17	12.8		Guatemala	9 - 30	16.1	1 - 21	10.2
	Mexico	9 - 14	11.0	13 - 15	13.6		Mexico	10 - 27	19.7	1 - 18	9.6

TABLE 6

Ranges of variations and averages of three measurements of the adult *Alouatta palliata* of the Panama series, separated into the 20 females and 10 males from Coiba island and the remaining 124 females and 47 males from other parts of Panama.

Measurement	Series	Females		Males	
		Range	Aver.	Range	Aver.
Length	Coiba island	62 - 71	66.6	67 - 73	70.9
	Panama without Coiba	62 - 77	69.5	65 - 80	74.4
Breadth	Coiba island	46 - 52	48.4	49 - 52	50.5
	Panama without Coiba	43 - 53	49.4	49 - 57	51.7
Height	Coiba island	37 - 40	38.7	38 - 40	39.0
	Panama without Coiba	36 - 42	38.2	35 - 42	38.8

None of the geographic or racial differences in cranial measurements within each of the three species under discussion are anywhere near as large as can be some of the sexual differences. The latter differences, as shown in the Tables 3 to 11, have been calculated as percentages of the averages for females in Table 12. From these data it is very evident that secondary sex differentiation is very much greater in *Alouatta* than in *Cebus* and that it is almost non-existent in *Ateles* among which many dimensions average actually less in males than in females. Even in regard to the thickness of the canine teeth the sexes differ in *Ateles* by only about 20 per cent of the female average, whereas in *Cebus* and *Alouatta* by more than 30 per cent. The arithmetic means of the relative sex differences in the first fourteen measurements in Table 12 amount to roughly 10·0 in *Alouatta*, 5·5 in *Cebus* and 0·7 in *Ateles*. The exactly corresponding values for *Colobus* monkeys are 4·1 in *C. polykomos*, 2·7 in *C. badius* and 3·5 in *C. verus* (Schultz, 1958) ; for chimpanzees this average equals 3·3 and for man 3·1 (Table 12). Judging by these few comparative data the sex differences in adult skulls are exceptionally marked in howler monkeys and unusually small in spider monkeys. Table 12 shows also that sex differences vary widely in intensity among these cranial dimensions. For instance, the breadth and height of the brain case is generally much closer alike in both sexes than the breadth and height of the face (bizygomatic breadth and nasion-prosthion). An especially large sex difference is found in the interorbital breadth in *Alouatta* and *Cebus*, the males of which having a proportionately broader interorbital region than could be expected merely from their larger general size. On the other hand, the average orbital height of males does not surpass that of females by an amount roughly corresponding to their

TABLE 7

Ranges of variations, averages, standard deviations, variation coefficients and their probable errors for seven cranial dimensions of adult *Cebus capucinus*. The numbers of specimens in these series are the same as given in Table 1.

Measurement	Series	Females				Males			
		Range	A ± E (A)	σ ± E (σ)	C ± E (C)	Range	A ± E (A)	σ ± E (σ)	C ± E (C)
Length	Panama	71 - 80	75.1 ± 0.24	2.29 ± 0.16	3.05 ± 0.22	73 - 85	79.0 ± 0.18	1.84 ± 0.12	2.33 ± 0.16
	Nicaragua	70 - 75	72.7 ± 0.32	1.65 ± 0.23	2.27 ± 0.31	72 - 78	76.4 ± 0.42	1.85 ± 0.29	2.42 ± 0.38
Breadth	Panama	49 - 57	52.1 ± 0.19	1.77 ± 0.13	3.40 ± 0.24	50 - 56	53.1 ± 0.13	1.38 ± 0.09	2.60 ± 0.18
	Nicaragua	50 - 55	52.4 ± 0.34	1.72 ± 0.24	3.28 ± 0.45	51 - 57	54.1 ± 0.39	1.73 ± 0.27	3.20 ± 0.51
Height	Panama	43 - 50	45.7 ± 0.18	1.67 ± 0.12	3.65 ± 0.26	44 - 51	47.1 ± 0.17	1.75 ± 0.12	3.71 ± 0.25
	Nicaragua	44 - 48	45.8 ± 0.22	1.13 ± 0.16	2.47 ± 0.34	46 - 49	46.9 ± 0.22	0.99 ± 0.16	2.11 ± 0.34
Basal length	Panama	51 - 60	54.5 ± 0.20	1.86 ± 0.13	3.41 ± 0.24	53 - 65	58.9 ± 0.28	2.92 ± 0.20	4.96 ± 0.34
	Nicaragua	50 - 55	53.0 ± 0.32	1.63 ± 0.22	3.07 ± 0.42	53 - 60	56.9 ± 0.51	2.28 ± 0.36	4.01 ± 0.64
Nasion-prosthion	Panama	29 - 34	31.9 ± 0.15	1.41 ± 0.10	4.42 ± 0.31	32 - 39	34.5 ± 0.17	1.74 ± 0.12	5.04 ± 0.34
	Nicaragua	30 - 34	32.0 ± 0.23	1.16 ± 0.16	3.63 ± 0.50	30 - 35	32.5 ± 0.40	1.79 ± 0.28	5.50 ± 0.87
Palatine length	Panama	30 - 36	33.1 ± 0.15	1.46 ± 0.10	4.41 ± 0.31	32 - 38	35.0 ± 0.14	1.41 ± 0.10	4.03 ± 0.27
	Nicaragua	32 - 34	32.5 ± 0.13	0.69 ± 0.10	2.12 ± 0.29	33 - 35	34.2 ± 0.20	0.89 ± 0.14	2.60 ± 0.41
Postcanine length	Panama	19 - 23	21.5 ± 0.10	0.99 ± 0.07	4.60 ± 0.33	21 - 24	22.0 ± 0.08	0.83 ± 0.04	3.77 ± 0.26
	Nicaragua	20 - 22	21.4 ± 0.15	0.79 ± 0.13	3.69 ± 0.51	21 - 23	21.7 ± 0.15	0.68 ± 0.11	3.13 ± 0.50

generally larger size, but is actually somewhat smaller in males than females in *Cebus*, *Ateles* and *Pan*. These findings appertaining to sexual differentiation will gain in interest with the addition of comparable data for other primates.

TABLE 8

Ranges of variations and averages of ten additional measurements of the same adult *Cebus capucinus* as in Table 7.

Measurement	Series	Females		Males	
		Range	Aver.	Range	Aver.
Basion-prosthion	Panama	58 - 66	62.0	60 - 76	68.1
	Nicaragua	56 - 62	59.3	60 - 70	64.2
Bizygomatic breadth	Panama	55 - 63	60.1	60 - 73	66.3
	Nicaragua	56 - 61	59.2	57 - 71	64.0
Biorbital breadth	Panama	48 - 56	52.5	50 - 65	56.7
	Nicaragua	48 - 54	51.0	50 - 59	54.7
Postorbital breadth	Panama	38 - 44	40.0	38 - 44	41.2
	Nicaragua	39 - 42	40.2	38 - 43	40.7
Interorbital breadth	Panama	3.5 - 6	4.9	4 - 8	5.7
	Nicaragua	4 - 6	4.9	5 - 7.5	5.8
Orbital height	Panama	18 - 22	20.0	18 - 22	19.8
	Nicaragua	20 - 22	20.5	19 - 22	20.3
Palatine breadth	Panama	27 - 33	30.1	30 - 34	31.7
	Nicaragua	28 - 30	29.2	28 - 32	30.1
Canine thickness	Panama	4.5 - 6	5.3	6 - 8	7.0
	Nicaragua	5 - 6	5.3	6 - 8	6.9
Mandibular length	Panama	52 - 60	55.9	55 - 68	61.9
	Nicaragua	51 - 57	54.2	54 - 65	58.9
Distance b. tempor.lin.	Panama	15 - 37	28.2	1 - 36	17.8
	Nicaragua	19 - 34	27.6	6 - 35	24.7

TABLE 9

Ranges of variations, averages, standard deviations, variation coefficients and their probable errors for seven cranial dimensions of adult *Ateles geoffroyi*. The numbers of specimens in these series are the same as given in Table 1.

Measurement	Series	Females				Males			
		Range	A ± E (A)	♂ ± E (♂)	C ± E (C)	Range	A ± E (A)	♂ ± E (♂)	C ± E (C)
Length	Panama	78 - 91	85.1 ± 0.23	2.73 ± 0.16	3.21 ± 0.19	80 - 91	85.9 ± 0.34	2.74 ± 0.24	3.19 ± 0.28
	Nicaragua	79 - 87	83.2 ± 0.29	2.15 ± 0.20	2.58 ± 0.24	79 - 89	83.6 ± 0.46	2.56 ± 0.32	3.06 ± 0.39
	Mexico	80 - 90	84.0 ± 0.42	2.35 ± 0.21	2.80 ± 0.25	79 - 91	85.2 ± 0.38	2.85 ± 0.26	3.34 ± 0.31
Breadth	Panama	54 - 63	59.1 ± 0.15	1.82 ± 0.11	3.08 ± 0.18	54 - 67	58.7 ± 0.33	2.65 ± 0.23	4.51 ± 0.39
	Nicaragua	55 - 61	58.0 ± 0.25	1.82 ± 0.17	3.14 ± 0.30	55 - 62	58.8 ± 0.35	1.96 ± 0.25	3.33 ± 0.42
	Mexico	53 - 60	58.1 ± 0.29	1.62 ± 0.15	2.79 ± 0.25	55 - 60	57.9 ± 0.20	1.49 ± 0.14	2.57 ± 0.24
Height	Panama	47 - 55	50.8 ± 0.15	1.81 ± 0.11	3.56 ± 0.21	48 - 55	50.4 ± 0.18	1.45 ± 0.13	2.88 ± 0.25
	Nicaragua	47 - 53	50.6 ± 0.21	1.59 ± 0.15	3.14 ± 0.30	49 - 53	50.5 ± 0.24	1.32 ± 0.17	2.61 ± 0.33
	Mexico	48 - 55	51.7 ± 0.30	1.69 ± 0.15	3.27 ± 0.29	49 - 58	52.8 ± 0.28	2.14 ± 0.20	4.05 ± 0.38
Basal length	Panama	54 - 66	61.7 ± 0.20	2.30 ± 0.14	3.73 ± 0.22	57 - 67	62.4 ± 0.30	2.41 ± 0.21	3.86 ± 0.34
	Nicaragua	58 - 65	61.8 ± 0.28	2.08 ± 0.20	3.37 ± 0.32	58 - 66	60.6 ± 0.39	2.17 ± 0.28	3.58 ± 0.45
	Mexico	56 - 64	60.4 ± 0.40	2.24 ± 0.20	3.71 ± 0.33	55 - 67	61.4 ± 0.39	2.96 ± 0.27	4.82 ± 0.45
Nasion - prosthion	Panama	32 - 42	37.2 ± 0.20	2.32 ± 0.14	6.23 ± 0.37	34 - 43	38.1 ± 0.30	2.45 ± 0.21	6.43 ± 0.56
	Nicaragua	33 - 40	36.9 ± 0.29	2.12 ± 0.20	5.74 ± 0.55	33 - 38	35.8 ± 0.24	1.36 ± 0.17	3.80 ± 0.48
	Mexico	33 - 41	36.7 ± 0.36	2.02 ± 0.18	5.51 ± 0.50	32 - 40	36.5 ± 0.22	1.70 ± 0.16	4.66 ± 0.43
Palatine length	Panama	33 - 42	37.0 ± 0.16	1.93 ± 0.12	5.22 ± 0.31	34 - 40	37.4 ± 0.22	1.75 ± 0.15	4.67 ± 0.41
	Nicaragua	33 - 38	35.4 ± 0.21	1.54 ± 0.15	4.35 ± 0.41	32 - 38	35.6 ± 0.30	1.64 ± 0.21	4.60 ± 0.58
	Mexico	33 - 38	36.2 ± 0.23	1.27 ± 0.11	3.51 ± 0.32	34 - 40	37.0 ± 0.23	1.72 ± 0.16	4.65 ± 0.43
Postcanine length	Panama	20 - 26	23.5 ± 0.10	1.13 ± 0.07	4.81 ± 0.29	21 - 25	23.1 ± 0.12	0.96 ± 0.08	4.15 ± 0.36
	Nicaragua	19 - 25	22.3 ± 0.18	1.32 ± 0.13	5.91 ± 0.56	19 - 24	22.1 ± 0.30	1.67 ± 0.21	7.55 ± 0.96
	Mexico	22 - 25	23.2 ± 0.15	0.81 ± 0.07	3.49 ± 0.31	22 - 24	22.9 ± 0.10	0.73 ± 0.07	3.18 ± 0.30

TABLE 10

Ranges of variations and averages of the same seven cranial dimensions as in Table 9 of the adult *Ateles geoffroyi* of the two smallest series. For number of specimens see Table 1.

Measurement	Series	Females		Males	
		Range	Aver	Range	Aver.
Length	Costa Rica	81 - 91	85.3	83 - 88	85.0
	Guatemala	84 - 84	84.0	82 - 85	83.7
Breadth	Costa Rica	55 - 62	58.1	55 - 64	58.7
	Guatemala	58 - 60	59.0	56 - 58	57.3
Height	Costa Rica	48 - 55	52.4	49 - 53	51.0
	Guatemala	52 - 54	52.7	49 - 51	50.0
Basal length	Costa Rica	60 - 67	62.6	60 - 65	62.7
	Guatemala	60 - 62	61.3	57 - 63	60.7
Nasion-prosthion	Costa Rica	36 - 39	37.6	34 - 43	39.2
	Guatemala	32 - 39	36.7	35 - 38	36.3
Palatine length	Costa Rica	34 - 37	35.4	34 - 38	36.5
	Guatemala	35 - 38	36.7	35 - 38	36.3
Postcanine length	Costa Rica	21 - 23	22.1	21 - 25	23.0
	Guatemala	23 - 23	23.0	23 - 23	23.0

The degree of variability in the absolute size of the cranial measurements is most accurately expressed by the variation coefficients for the largest of the series, as listed in the Tables 3, 7 and 9. In order to be able to answer the basic question of whether or not there are species differences in variability, the means of all coefficients for each species are compared in Table 13. It is seen that *Cebus capucinus* is generally somewhat less variable than the other two species of Central American primates and that all three species are less variable than the *Colobus* monkeys for which exactly comparable data are available. It is mentioned also that the latter monkeys are all from one very limited region in contrast to some of the series of the present report. Table 13 demonstrates furthermore that in every one of these species the males are slightly more variable than the corresponding females.

In Table 14 the means of the variation coefficients for the main dimensions of the neurocranium are contrasted with those for the splanchnocranium with

TABLE 11

Ranges of variations and averages of ten additional measurements of the same adult *Ateles geoffroyi* as in Tables 9 and 10.

Measurement	Series	Females		Males		Measurement	Series	Females		Males	
		Range	Aver.	Range	Aver.			Range	Aver.	Range	Aver.
Basion - prosthion	Panama	65 - 82	75.8	70 - 86	76.5	Orbital height	Panama	20 - 25	22.2	20 - 25	21.9
	Costa Rica	71 - 81	74.7	72 - 80	77.2		Costa Rica	22 - 24	22.7	21 - 26	23.0
	Nicaragua	70 - 80	75.0	70 - 79	73.8		Nicaragua	21 - 25	22.8	21 - 24	22.5
	Guatemala	72 - 78	75.7	69 - 76	73.7		Guatemala	22 - 23	22.3	21 - 23	21.7
	Mexico	67 - 79	74.0	67 - 80	74.8		Mexico	20 - 24	22.1	20 - 24	22.1
Bizygomatic breadth	Panama	60 - 74	67.2	64 - 74	69.7	Palatine breadth	Panama	29 - 35	32.0	30 - 34	32.0
	Costa Rica	64 - 71	67.7	65 - 72	69.5		Costa Rica	29 - 33	31.6	31 - 33	32.5
	Nicaragua	61 - 69	65.0	60 - 70	67.0		Nicaragua	29 - 33	30.8	29 - 33	30.8
	Guatemala	64 - 69	65.7	62 - 68	65.0		Guatemala	31 - 32	31.7	30 - 30	30.0
	Mexico	58 - 67	63.3	58 - 72	66.7		Mexico	28 - 33	31.0	30 - 33	31.3
Biorbital breadth	Panama	54 - 66	60.2	55 - 64	59.7	Canine thickness	Panama	4.5 - 6.5	5.5	5.5 - 7	6.6
	Costa Rica	56 - 65	61.6	58 - 64	61.5		Costa Rica	4.5 - 6	5.1	6 - 7	6.5
	Nicaragua	57 - 65	56.0	55 - 62	58.8		Nicaragua	4.5 - 6	5.2	5.5 - 7	6.2
	Guatemala	55 - 62	59.0	52 - 61	56.3		Guatemala	4.5 - 5	4.8	6 - 7	6.3
	Mexico	53 - 61	56.3	53 - 65	57.7		Mexico	4.5 - 6	5.0	5.5 - 7	6.1
Postorbital breadth	Panama	43 - 53	47.8	45 - 52	48.2	Mandibular length	Panama	60 - 75	68.7	64 - 78	69.9
	Costa Rica	45 - 51	48.0	45 - 50	47.0		Costa Rica	64 - 73	67.0	63 - 72	69.0
	Nicaragua	44 - 52	48.0	45 - 50	47.4		Nicaragua	61 - 71	65.9	62 - 70	65.2
	Guatemala	46 - 49	47.7	46 - 48	47.0		Guatemala	63 - 69	66.7	62 - 68	65.3
	Mexico	45 - 49	46.7	44 - 53	47.6		Mexico	59 - 70	65.1	59 - 71	65.9
Interorbital breadth	Panama	7 - 11	8.7	7 - 11	9.0	Distance b. tempor.lin.	Panama	26 - 51	39.8	17 - 48	33.0
	Costa Rica	8 - 10	9.7	7 - 10	9.2		Costa Rica	29 - 45	38.3	20 - 43	29.5
	Nicaragua	8 - 10	8.8	8 - 10	8.9		Nicaragua	31 - 47	39.0	28 - 43	36.2
	Guatemala	8 - 9	8.7	7 - 9.5	8.5		Guatemala	37 - 45	39.7	35 - 41	37.0
	Mexico	7 - 10	8.7	7 - 11	9.0		Mexico	35 - 46	40.3	29 - 47	37.2

TABLE 12

Sex differences in average measurements, expressed as percentages of averages of females, in adult *Alouatta*, *Cebus* and *Ateles* and for comparison in adult chimpanzee and man (see Table 22). + = ♂ > ♀. — = ♂ < ♀.

Measurement :	*Alouatta palliata*			*Cebus capucinus*		*Ateles geoffroyi*			Chimpanzee	Man
	Panama	Nicaragua	Mexico	Panama	Nicaragua	Panama	Nicaragua	Mexico		
Length	+ 6.8	+ 7.2	+ 9.1	+ 5.2	+ 5.1	+ 0.9	+ 0.5	+ 1.4	+ 3.1	+ 4.2
Breadth	+ 4.3	+ 4.8	+ 3.9	+ 1.9	+ 3.2	- 0.7	+ 1.4	- 0.3	+ 3.0	+ 4.6
Height	+ 1.3	+ 1.1	+ 2.3	+ 3.1	+ 2.4	- 0.8	- 0.2	+ 2.1	+ 4.5	+ 3.8
Basal length	+ 11.1	+ 11.0	+ 14.8	+ 8.1	+ 7.4	+ 1.1	- 1.9	+ 1.7	+ 1.1	+ 6.6
Basion-prosthion	+ 13.6	+ 15.3	+ 18.9	+ 9.8	+ 8.3	+ 0.9	- 1.6	+ 1.1	+ 3.4	+ 4.5
Nasion-prosthion	+ 12.1	+ 13.8	+ 13.2	+ 8.1	+ 1.6	+ 2.4	- 3.0	- 0.5	+ 4.8	+ 7.2
Bizygomatic breadth	+ 14.5	+ 17.0	+ 18.4	+ 10.3	+ 8.1	+ 3.7	+ 3.1	+ 5.4	+ 9.7	+ 6.0
Biorbital breadth	+ 13.7	+ 17.0	+ 14.6	+ 8.0	+ 7.2	- 0.8	+ 5.0	+ 2.5	+ 4.1	+ 3.3
Postorbital breadth	+ 1.7	+ 2.0	+ 0.2	+ 3.0	+ 1.2	+ 0.8	- 1.2	+ 1.9	- 1.1	+ 1.7
Interorbital breadth	+ 17.7	+ 22.8	+ 23.6	+ 16.3	+ 18.3	+ 3.4	+ 1.1	+ 3.4	+ 4.4	- 0.4
Orbital height	+ 3.8	+ 4.7	+ 6.0	- 1.0	- 1.0	- 1.4	- 1.3	0	- 0.6	+ 0.3
Palatine length	+ 10.3	+ 10.6	+ 11.2	+ 5.7	+ 5.2	+ 1.1	+ 0.6	+ 2.2	+ 4.0	+ 1.9
Palatine breadth	+ 8.1	+ 9.6	+ 11.4	+ 5.3	+ 3.1	0	0	+ 1.0	+ 2.9	+ 3.1
Postcanine length	+ 6.2	+ 6.0	+ 6.0	+ 2.3	+ 1.4	- 1.7	- 0.9	- 1.3	+ 3.2	- 3.7
Average of above 14 measurements	+ 8.9	+ 10.2	+ 11.0	+ 6.1	+ 5.1	+ 0.6	+ 0.1	+ 1.5	+ 3.3	+ 3.1
C. thickness	+ 35.0	+ 32.2	+ 32.2	+ 32.1	+ 30.2	+ 20.0	+ 19.2	+ 22.0	-	-
Mandibular length	+ 13.4	+ 15.7	+ 18.3	+ 10.7	+ 8.7	+ 1.7	- 1.1	+ 1.2	+ 4.9	+ 4.1

the result that it becomes very evident that the face part of the skull is significantly more variable than the brainpart in our platyrrhines, as it was found to be in the catarrhine *Colobus* monkeys.

TABLE 13

The arithmetic means of the variation coefficients for the seven measurements in the Tables 3, 7 and 9 and for comparison the exactly corresponding data for *Colobus* (after Schultz, 1958).

Species	♀	♂
Alouatta palliata	3.66	4.08
Cebus capucinus	3.39	3.53
Ateles geoffroyi	3.96	4.07
Colobus polykomos	4.35	4.73
Colobus badius	4.01	4.37
Colobus verus	4.03	4.13

TABLE 14

The arithmetic means of the variation coefficients in the Tables 3, 7 and 9 for the four measurements of the neurocranium and for the three measurements of the splanchnocranium and for comparison the exactly corresponding data for *Colobus* (after Schultz, 1958). The sexes have been combined and so have all the *Colobus* in calculating these means.

Genus	Neurocranium	Splanchnocranium
Alouatta	3.33	4.59
Cebus	3.12	3.91
Ateles	3.34	4.91
Colobus	3.55	5.22

CRANIAL INDICES AND FORM OF FOREHEAD OF ADULTS

Six cranial indices have been selected of which three appertain to the neurocranium and the others to the splanchnocranium. The averages and the variability of these indices in the larger series are shown in the Tables 15, 16 and 17. The first index gives the length-width proportion of the braincase for which frequency polygons have been constructed in Fig. 1. All three of our platyrrhine species are on an average decidedly dolichocran and many individual specimens are even ultradolichocran. The geographic series can differ slightly within a species, as e.g. the Mexican howlers which tend to have

TABLE 15

Ranges of variations, averages, standard deviations, variation coefficients and their probable errors for six cranial proportions of adult *Alouatta palliata*. The numbers of specimens in these series are the same as given in Table 1.

Index	Series	Females				Males			
		Range	A ± E (A)	♂ ± E (♂)	C ± E (C)	Range	A ± E (A)	♂ ± E (♂)	C ± E (C)
Breadth / Length	Panama	64.2 - 77.4	71.4 ± 0.15	2.66 ± 0.11	3.72 ± 0.15	64.6 - 76.9	69.8 ± 0.25	2.83 ± 0.18	4.05 ± 0.25
	Nicaragua	67.6 - 75.4	71.7 ± 0.15	1.67 ± 0.10	2.33 ± 0.14	65.4 - 77.1	70.1 ± 0.20	2.09 ± 0.14	2.98 ± 0.20
	Mexico	65.3 - 74.3	69.7 ± 0.42	2.89 ± 0.30	4.14 ± 0.43	61.3 - 70.7	66.3 ± 0.55	2.59 ± 0.39	3.91 ± 0.59
Height / Length	Panama	49.3 - 65.6	55.5 ± 0.16	2.82 ± 0.11	5.08 ± 0.20	47.4 - 59.7	52.7 ± 0.24	2.65 ± 0.17	5.03 ± 0.32
	Nicaragua	52.1 - 57.6	54.2 ± 0.12	1.34 ± 0.08	2.47 ± 0.15	47.4 - 55.7	51.1 ± 0.16	1.66 ± 0.11	3.25 ± 0.22
	Mexico	52.8 - 62.7	56.0 ± 0.40	2.70 ± 0.28	4.82 ± 0.50	48.7 - 55.6	52.5 ± 0.46	2.15 ± 0.32	4.09 ± 0.62
Basal l. / Length	Panama	81.2 - 91.5	86.1 ± 0.12	2.20 ± 0.09	2.55 ± 0.10	84.5 - 94.0	89.3 ± 0.19	2.17 ± 0.14	2.43 ± 0.15
	Nicaragua	80.0 - 92.3	85.1 ± 0.18	2.07 ± 0.13	2.43 ± 0.15	84.0 - 94.6	88.0 ± 0.21	2.19 ± 0.15	2.49 ± 0.17
	Mexico	84.1 - 92.7	87.5 ± 0.36	2.44 ± 0.25	2.79 ± 0.29	85.7 - 98.6	92.2 ± 0.81	3.79 ± 0.57	4.11 ± 0.62
Palatine l. / Length	Panama	49.3 - 64.6	58.9 ± 0.12	2.23 ± 0.09	3.78 ± 0.15	55.0 - 67.2	60.8 ± 0.22	2.51 ± 0.16	4.13 ± 0.26
	Nicaragua	54.9 - 63.2	59.5 ± 0.18	2.10 ± 0.13	3.53 ± 0.22	58.1 - 65.3	61.5 ± 0.28	1.83 ± 0.12	2.97 ± 0.20
	Mexico	55.6 - 63.9	59.7 ± 0.33	2.24 ± 0.23	3.75 ± 0.39	56.6 - 64.4	60.8 ± 0.43	2.03 ± 0.31	3.34 ± 0.50
Nas.-prosth. / Bizygom. br.	Panama	45.9 - 58.3	51.7 ± 0.13	2.24 ± 0.09	4.33 ± 0.17	46.4 - 56.8	50.6 ± 0.19	2.13 ± 0.13	4.21 ± 0.26
	Nicaragua	47.9 - 58.1	52.9 ± 0.18	2.13 ± 0.13	4.02 ± 0.25	45.8 - 55.3	51.3 ± 0.23	2.45 ± 0.16	4.77 ± 0.32
	Mexico	48.6 - 62.9	56.9 ± 0.61	4.15 ± 0.43	7.29 ± 0.76	45.7 - 61.7	54.4 ± 1.08	5.05 ± 0.76	9.28 ± 1.40
Orbital h. / Nas.-prosth.	Panama	51.2 - 67.6	59.3 ± 0.15	2.74 ± 0.11	4.62 ± 0.18	48.8 - 62.2	54.7 ± 0.30	3.34 ± 0.21	6.11 ± 0.38
	Nicaragua	51.2 - 64.7	57.6 ± 0.23	2.59 ± 0.16	4.49 ± 0.28	47.8 - 60.5	53.0 ± 0.27	2.79 ± 0.19	5.26 ± 0.35
	Mexico	50.0 - 61.1	55.8 ± 0.48	3.25 ± 0.34	5.82 ± 0.61	46.0 - 62.2	52.3 ± 1.02	4.75 ± 0.72	9.08 ± 1.37

TABLE 16

Ranges of variations, averages, standard deviations, variation coefficients and their probable errors for six cranial proportions of adult *Cebus capucinus*. The numbers of specimens in these series are the same as given in Table 1.

Index	Series	Females				Males			
		Range	A ± E (A)	σ ± E (σ)	C ± E (C)	Range	A ± E (A)	σ ± E (σ)	C ± E (C)
Breadth / Length	Panama	64.9 - 74.3	69.3 ± 0.24	2.31 ± 0.16	3.33 ± 0.24	63.4 - 72.7	67.2 ± 0.23	2.39 ± 0.16	3.56 ± 0.24
	Nicaragua	67.6 - 77.1	72.2 ± 0.65	3.35 ± 0.46	4.64 ± 0.64	67.5 - 73.3	70.8 ± 0.46	2.04 ± 0.32	2.88 ± 0.46
Height / Length	Panama	57.1 - 64.9	60.9 ± 0.19	1.83 ± 0.13	3.01 ± 0.21	54.3 - 65.7	59.6 ± 0.21	2.20 ± 0.15	3.69 ± 0.25
	Nicaragua	60.8 - 67.1	63.1 ± 0.38	1.93 ± 0.27	3.06 ± 0.42	59.7 - 63.9	61.3 ± 0.31	1.39 ± 0.22	2.27 ± 0.36
Basal l. / Length	Panama	68.3 - 76.9	72.5 ± 0.22	2.14 ± 0.15	2.95 ± 0.21	68.8 - 79.8	74.6 ± 0.25	2.65 ± 0.18	3.55 ± 0.24
	Nicaragua	69.3 - 76.4	72.9 ± 0.40	2.03 ± 0.28	2.78 ± 0.38	70.7 - 77.9	74.4 ± 0.48	2.14 ± 0.34	2.88 ± 0.46
Palatine l. / Length	Panama	40.3 - 47.3	44.2 ± 0.16	1.57 ± 0.11	3.55 ± 0.25	41.2 - 48.1	44.3 ± 0.15	1.54 ± 0.10	3.48 ± 0.24
	Nicaragua	42.7 - 47.2	44.7 ± 0.26	1.36 ± 0.19	3.04 ± 0.42	43.4 - 45.8	44.8 ± 0.17	0.74 ± 0.12	1.65 ± 0.26
Nas.-prosth. / Bizygom. br.	Panama	46.0 - 58.6	53.1 ± 0.29	2.76 ± 0.20	5.20 ± 0.37	47.1 - 56.4	52.2 ± 0.22	2.29 ± 0.16	4.39 ± 0.30
	Nicaragua	52.5 - 56.7	54.1 ± 0.48	1.33 ± 0.18	2.46 ± 0.34	47.8 - 54.8	51.8 ± 0.50	2.22 ± 0.35	4.28 ± 0.68
Orbital h. / Nas.-prosth.	Panama	55.9 - 75.9	62.9 ± 0.41	3.90 ± 0.28	6.20 ± 0.44	48.7 - 66.7	57.6 ± 0.36	3.77 ± 0.26	6.54 ± 0.44
	Nicaragua	58.8 - 70.0	64.1 ± 0.57	2.90 ± 0.40	4.53 ± 0.63	54.3 - 66.7	61.5 ± 0.77	3.42 ± 0.54	5.56 ± 0.88

TABLE 17

TABLE 17

Ranges of variations, averages, standard deviations, variation coefficients and their probable errors for six cranial proportions of adult *Ateles geoffroyi*. The numbers of specimens in these series are the same as given in Table 1.

Index	Series	Females				Males			
		Range	A ± E (A)	σ ± E (σ)	C ± E (C)	Range	A ± E (A)	σ ± E (σ)	C ± E (C)
Breadth / Length	Panama	62.2 - 76.5	69.4 ± 0.23	2.75 ± 0.16	3.96 ± 0.24	63.3 - 75.3	68.3 ± 0.37	3.02 ± 0.26	4.42 ± 0.38
	Nicaragua	64.7 - 74.1	69.8 ± 0.34	2.51 ± 0.24	3.60 ± 0.34	65.9 - 75.6	70.4 ± 0.60	3.36 ± 0.43	4.77 ± 0.60
	Mexico	63.1 - 72.8	69.3 ± 0.49	2.70 ± 0.24	3.89 ± 0.35	63.6 - 73.8	67.9 ± 0.30	2.26 ± 0.21	3.33 ± 0.31
Height / Length	Panama	55.6 - 64.6	59.8 ± 0.20	2.36 ± 0.14	3.95 ± 0.24	53.9 - 62.5	58.8 ± 0.24	1.95 ± 0.17	3.32 ± 0.29
	Nicaragua	55.8 - 64.6	60.8 ± 0.35	2.62 ± 0.25	4.31 ± 0.41	57.0 - 64.6	60.4 ± 0.37	2.03 ± 0.26	3.36 ± 0.43
	Mexico	57.8 - 65.0	61.6 ± 0.35	1.92 ± 0.17	3.12 ± 0.28	56.7 - 66.7	62.0 ± 0.30	2.27 ± 0.21	3.66 ± 0.34
Basal l. / Length	Panama	65.9 - 78.1	72.5 ± 0.19	2.24 ± 0.13	3.09 ± 0.19	68.2 - 78.8	72.7 ± 0.29	2.32 ± 0.20	3.19 ± 0.28
	Nicaragua	70.7 - 78.7	74.2 ± 0.25	1.84 ± 0.17	2.48 ± 0.24	70.7 - 77.2	72.6 ± 0.31	1.70 ± 0.22	2.34 ± 0.30
	Mexico	67.5 - 76.5	71.9 ± 0.33	1.83 ± 0.16	2.54 ± 0.23	67.1 - 74.4	72.4 ± 0.26	1.96 ± 0.18	2.71 ± 0.25
Palatine l. / Length	Panama	38.4 - 48.3	43.5 ± 0.19	2.24 ± 0.13	5.15 ± 0.31	39.5 - 47.6	43.6 ± 0.24	1.92 ± 0.17	4.40 ± 0.38
	Nicaragua	39.3 - 45.7	42.5 ± 0.24	1.77 ± 0.17	4.17 ± 0.40	39.0 - 46.8	42.7 ± 0.37	2.06 ± 0.26	4.82 ± 0.61
	Mexico	40.2 - 46.3	43.1 ± 0.27	1.48 ± 0.13	3.43 ± 0.31	40.2 - 48.8	43.4 ± 0.22	1.64 ± 0.15	3.78 ± 0.35
Nas.-prosth. / Bizygom. br.	Panama	47.1 - 65.6	55.4 ± 0.30	3.49 ± 0.21	6.30 ± 0.38	49.3 - 61.4	54.6 ± 0.36	2.94 ± 0.26	5.38 ± 0.47
	Nicaragua	50.7 - 60.3	55.6 ± 0.37	2.73 ± 0.26	4.91 ± 0.47	50.0 - 58.3	53.5 ± 0.40	2.22 ± 0.28	4.15 ± 0.53
	Mexico	52.3 - 63.8	58.1 ± 0.51	2.86 ± 0.26	4.92 ± 0.44	48.6 - 60.6	54.8 ± 0.40	3.04 ± 0.28	5.54 ± 0.52
Orbital h. / Nas.-prosth.	Panama	50.0 - 75.0	59.9 ± 0.32	3.74 ± 0.22	6.24 ± 0.37	48.8 - 68.6	57.7 ± 0.47	3.86 ± 0.34	6.69 ± 0.58
	Nicaragua	57.9 - 70.6	63.2 ± 0.43	3.17 ± 0.30	5.01 ± 0.48	58.3 - 67.7	63.4 ± 0.52	2.92 ± 0.37	4.61 ± 0.59
	Mexico	53.7 - 70.6	60.3 ± 0.71	3.94 ± 0.35	6.53 ± 0.59	55.0 - 68.8	60.7 ± 0.38	2.91 ± 0.27	4.79 ± 0.45

relatively narrower brain cases than the Nicaraguan and Panamanian howlers, but the respective ranges of variations overlap so extensively that the average differences have little significance. With only one exception the averages of males are smaller than those of females of the same local series, a sex difference corresponding to that found in man. The distribution of the individual variations within the series is somewhat irregular, especially among males, according to Fig. 1. This may be due to the changes with age among adults in the measurements forming this index, which will be discussed later.

The second index in the tables expresses the height of the brain case in per cent of its length. This relative height is significantly smaller in howlers than in capuchin and spider monkeys and smaller in males than in females. This sex difference is most marked in howlers and capuchin monkeys, whereas small and not constant in spider monkeys, in which there are few marked secondary sex characters of any kind. The geographic differences among the averages of this length-height index can hardly be regarded as racial ones in view of the extensive overlapping of the ranges of variations in the different local series of the same species.

The third index—the proportionate length of the skull base—is an expression for the relative position of the foramen magnum, i.e., its oral border at the basion. The higher this index the farther aborally lies the cranio-vertebral joint and *vice versa*. The values for this index are consistently much higher in *Alouatta* than in the two other platyrrhines under investigation and the highest of all these indices are found among the Mexican howlers. In *Alouatta* and in *Cebus* the average relative basal length is always higher in males than in females, but in *Ateles* there is no such consistent sex difference, a result which agrees fully with previous findings of the author (1955) by means of a slightly different method.

The relative palatine length (fourth index in the Tables 15 to 17) is also much greater in *Alouatta* than in *Cebus* and *Ateles* and there are no noteworthy racial differences in this index. It is surprising that only in *Alouatta* do the males have a relatively longer palate than the females, whereas in *Cebus* and *Ateles* this proportion is practically alike in both sexes in spite of the larger canines in males (see Table 12).

The fifth index of the Tables 15 to 17 expresses the height of the face in relation to its width and amounts on an average in all series to slightly more than fifty. In *Alouatta* this index tends to be especially high in both sexes of the Mexican series. The data reveal a consistent sex difference, according to which the face is proportionately lower in males than in females, largely due to the smaller bizygomatic breadth of the latter.

The last index in these tables shows the relative height of the orbit which is considerably smaller in *Alouatta* than in the other two species. In view of the very extensive ranges of variations of this index none of the average differences among the geographic series can be regarded as being really significant. A sex difference, however, is well marked in *Alouatta* and *Cebus* in which males have on an average relatively lower orbits than females.

The degree of variability in these indices is most accurately expressed by the variation coefficients which permit some generalizations, based upon the means

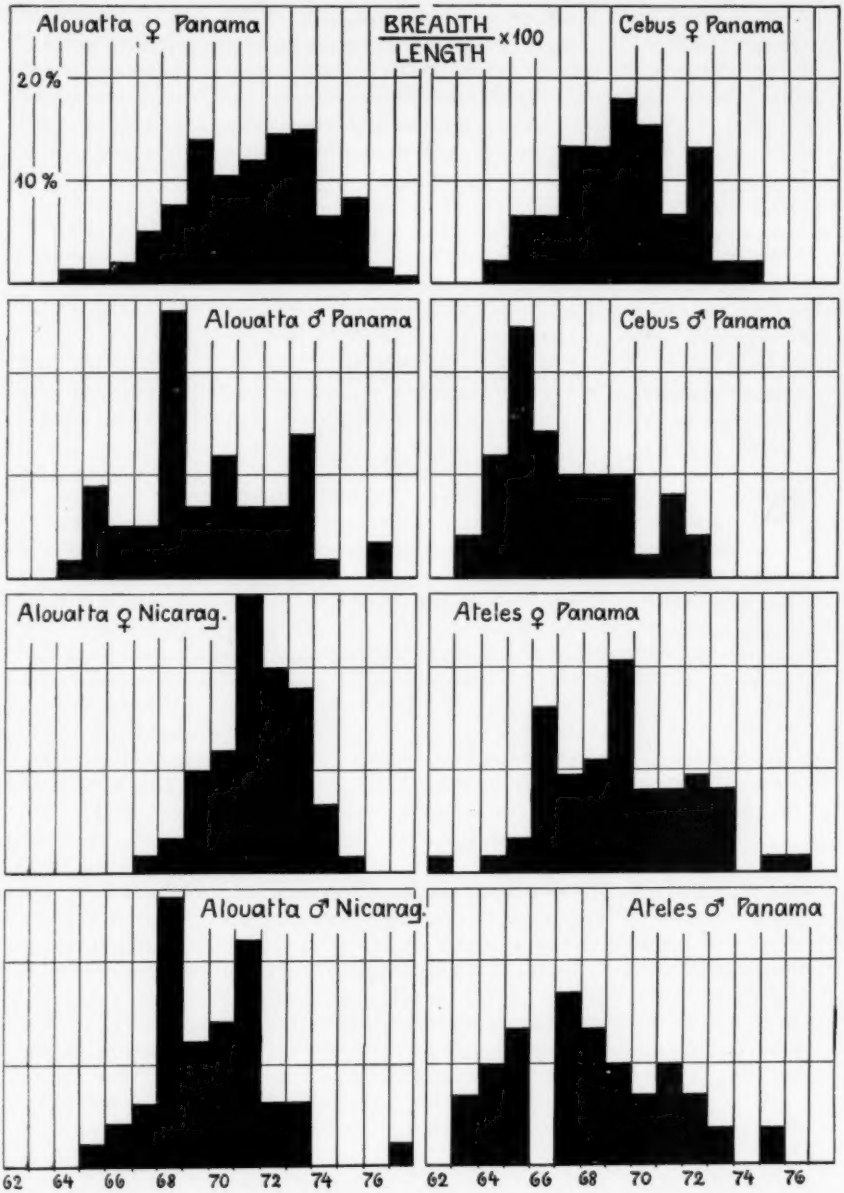

Fig. 1.—Frequency polygons of the individual variations in the length-breadth index in the largest series of adults. The numbers of cases in each column of 1·9 index units are shown as percentages of the total number of cases.

listed in Table 18. In regard to cranial proportions *Cebus capucinus* is slightly less variable than the other two species which are generally about as variable as *Colobus* monkeys. It may be recalled here that in regard to *absolute* measurements *Cebus* was found to be decidedly less variable than the other two and that the mean coefficients of all three species are considerably smaller than those of *Colobus* (see Table 13). It is of interest also that the Nicaraguan series

TABLE 18

Some arithmetic means of the variation coefficients for the six indices in Tables 15, 16 and 17, and for comparison exactly corresponding data for *Colobus* monkeys from Liberia after Schultz (1958).

Mean of indices for:	Alouatta	Cebus	Ateles	Colobus
Panama series (♀ + ♂)	4.17	4.12	4.67	badius 4.41
Nicaragua series (♀ + ♂)	3.42	3.34	4.04	verus 4.48
Mexico series (♀ + ♂)	5.20	-	4.02	polyk. 4.77
Females of all series	4.00	3.73	4.31	4.61
Males of all series	4.53	3.73	4.18	4.50
Three indices of neurocranium (♀ + ♂)	3.48	3.22	3.45	3.46
Three indices of splanchnocranium (♀ + ♂)	5.04	4.24	5.05	5.65

of all three platyrrhine species, which had been collected by the author in a very limited region, are not nearly as variable as the corresponding Panamanian series, which are composed of specimens representing a much larger area. This, however, does not necessarily support the assumption of several races of each species in Panama, because the Mexican howlers are even more variable than the Panamanian ones, whereas the Mexican spider monkeys are the least variable ones, and no taxonomist has ever claimed different Mexican races among those platyrrhines of their northernmost limit of distribution.

The absolute cranial measurements are more variable in males than in females, as has been shown by Table 13, but such a sex difference for relative measurements exists only in *Alouatta* according to Table 18. The latter table gives also the data in support of the conclusion that the proportions appertaining to the face are very much more variable than those of the brainpart of the skull, a difference which had already been found in connection with the discussion of the absolute measurements (Table 14).

There occur a great many variations in the form of cranial parts which are difficult to express metrically or, at least, would increase the tabular matter in this report unduely. The author (1926) has already called attention to the often astoundingly marked individual variations in such features as the shape of the nasal bones and the curvature of the facial profile among the monkeys from one locality in Nicaragua. Here it must suffice to show briefly a few of

the extreme variations in the midsagittal curvature of the frontal region in *Ateles* by means of the examples in Fig. 2. In many cases one encounters a bulging, real forehead whereas in other skulls from the same locality the frontal bone recedes above the orbits in a flat curve. In the former instances the nearly globular braincase, typical of infantile spider monkeys (Schultz, 1926, Fig. 8), has been retained much more closely than in the latter "low-brows". On the basis of these findings the writer feels that the diagnostic or taxonomic significance of the detailed shape of the forehead in the fossil skulls of early man is perhaps not as reliable as some authors have assumed and, at any rate, that the degree of bulging of the forehead might have been as variable in fossil man as in recent spider monkeys, which have acquired the most highly developed brains among all New World primates. It is finally to be mentioned here also that in the howling and capuchin monkeys the curvature of the forehead is nowhere near as variable as in the spider monkeys, but the thickness and prominence of the supraorbital rim and glabellar region varies individually to a very marked degree.

AGE CHANGES IN CRANIAL MEASUREMENTS

The available material contains an adequate number of infantile and juvenile specimens for a comparative survey of post-natal changes in the skull with special consideration of the *relative* amount of change in the different dimensions as well as in the different species. In order to gain some preliminary scale for evaluating these *relative* age changes, a series of chimpanzee skulls and one of human skulls has also been measured and analyzed in a strictly corresponding manner. The condensed results are represented by the data in the Tables 19 to 22, which are best discussed all together. Of the three main diameters of the brain case the length increases with growth most and the breadth least in all three platyrrhine species as well as in chimpanzee and man, though in chimpanzees there is practically no difference between the increase in breadth and height. In *Cebus* the breadth of adults is even slightly smaller than that of younger specimens. These findings indicate that the braincase becomes proportionately narrower with growth in all of these primates. The total percentage increase in the length of the skull base is much greater than that of the cranial vault in all series, showing that the basion (and the occipital condyles) shifts with growth to a more aboral position, as in all other simian primates (Schultz, 1955).

The basion-prosthion and nasion-prosthion distances increase with age by much greater relative amounts than any of the measurements mentioned above. This shows that postnatally the face not only grows more intensively than the braincase, but also projects continually farther forward, as it is the general rule among all primates (Schultz, 1955). With the three measurements, basal length, basion-prosthion distance and facial height, the triangles in Fig. 3 have been constructed which show accurately the age changes in the degrees of prognathism. It is seen that in all three of our platyrrhine species the prosthion shifts orally with growth and this most of all in *Alouatta*, especially in males. In *Cebus* the typically infantile, orthognath direction of the facial axis is retained to adult life.

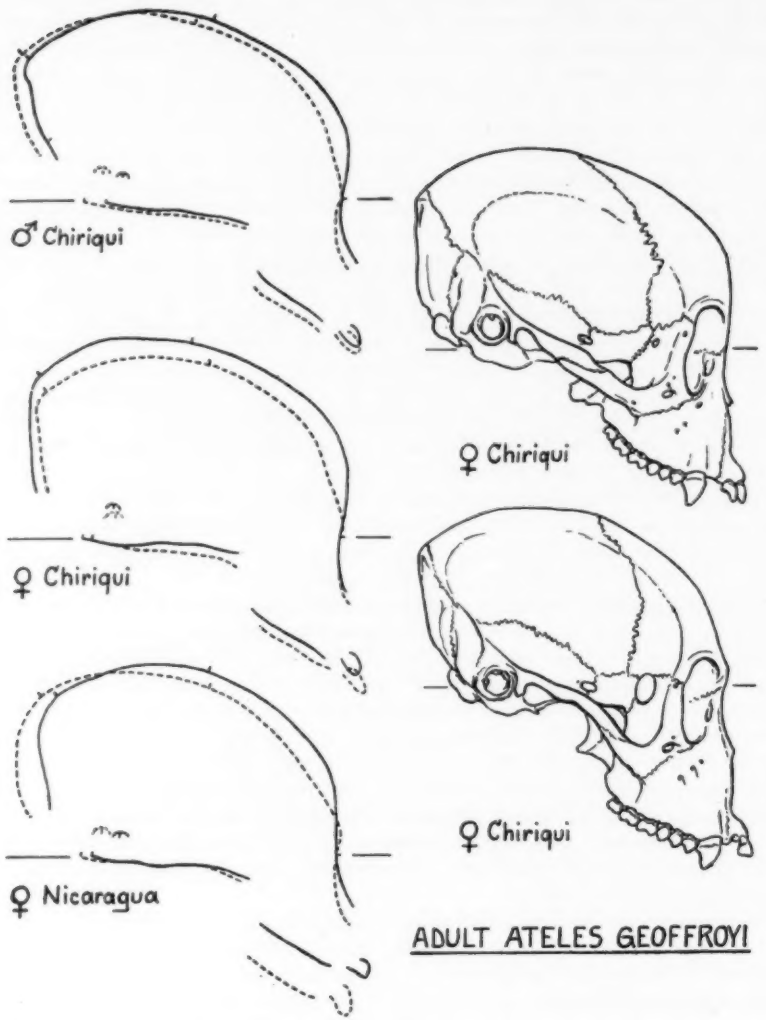

Fig. 2.—Midsagittal sections and dioptrographic side views of some skulls of adult *Ateles*, six from Chiriqui, Panama and two from Nicaragua, oriented in the nasion-basion horizon, to show the very marked variations in particularly the curvature of the forehead among specimens of the same local series and sex. Note also the difference in the size of the foramen in the orbital plate of the zygomatic bone in the two skulls on the right.

TABLE 19

Averages of some measurements at different ages and the total age change of these measurements, expressed as percentage of the averages for infants, in *Alouatta palliata* of Panama.

Measurement	Sex	Infants 9 ♀ 8 ♂	Juven. I 14 ♀ 8 ♂	Juven. II 11 ♀ 14 ♂	Adults 144 ♀ 57 ♂	% Change
Length	♀	59.2	61.8	65.9	69.1	+ 16.7
	♂	59.6	65.0	67.3	73.8	+ 23.8
Breadth	♀	47.6	47.8	48.8	49.3	+ 3.6
	♂	48.1	49.6	50.7	51.4	+ 6.8
Height	♀	36.0	36.9	37.3	38.3	+ 6.4
	♂	37.0	37.6	37.7	38.8	+ 4.9
Basal length	♀	44.3	48.1	54.1	59.4	+ 34.1
	♂	45.2	51.6	55.9	66.0	+ 46.0
Basion-prosthion	♀	50.3	59.0	70.1	81.1	+ 61.2
	♂	53.5	64.2	72.9	92.1	+ 72.1
Nasion-prosthion	♀	22.9	27.8	32.2	36.4	+ 58.9
	♂	23.7	28.7	33.2	40.8	+ 72.2
Bizygomatic breadth	♀	44.8	52.3	62.1	70.5	+ 57.4
	♂	47.0	58.0	63.7	80.7	+ 71.7
Biorbital breadth	♀	39.7	43.9	51.2	58.4	+ 47.1
	♂	40.7	47.7	52.1	66.4	+ 63.1

Measurements	Sex	Infants 9 ♀ 8 ♂	Juven. I 14 ♀ 8 ♂	Juven. II 11 ♀ 14 ♂	Adults 144 ♀ 57 ♂	% Change
Postorbital breadth	♀	38.9	39.3	40.2	40.0	+ 2.8
	♂	38.5	40.2	40.8	40.7	+ 5.7
Interorbital breadth	♀	5.7	6.2	7.7	9.6	+ 68.4
	♂	6.0	7.0	7.8	11.3	+ 88.3
Orbital height	♀	17.2	18.8	20.3	21.5	+ 25.0
	o	17.0	19.8	20.8	22.3	+ 31.2
Palatine length	♀	23.2	29.1	35.5	40.6	+ 75.0
	♂	25.2	30.5	36.9	44.8	+ 77.7
Palatine breadth	♀	25.7	31.3	35.2	37.1	+ 44.4
	o	28.5	33.2	36.1	40.1	+ 40.7
Postcanine length	♀	13.3	20.0	24.6	30.8	+131.5
	♂	14.2	20.4	26.8	32.7	+130.2
Mandibular length	♀	43.9	53.6	64.9	75.1	+ 71.1
	♂	47.5	58.1	66.9	85.2	+ 79.4
Average of % changes	♀	-	-	-	-	+ 46.9
	♂	-	-	-	-	+ 54.3

TABLE 20

Averages of some measurements at different ages and the total age change of these measurements, expressed as percentage of the averages for infants, in *Cebus capucinus* of Panama.

Measurement	Sex	Infants 3 ♀ 4 ♂	Juven. I 5 ♀ 5 ♂	Juven. II 9 ♀ 12 ♂	Adults 45 ♀ 49 ♂	% Change
Length	♀	69.7	72.2	72.8	75.1	+ 7.7
	♂	72.2	72.2	74.8	79.0	+ 9.4
Breadth	♀	53.7	53.2	53.3	52.1	- 3.0
	♂	55.5	54.2	54.3	53.1	- 4.3
Height	♀	43.0	45.2	45.0	45.7	+ 6.3
	♂	46.0	44.0	46.8	47.1	+ 2.4
Basal length	♀	44.3	48.4	49.7	54.5	+ 23.0
	♂	47.0	47.2	52.4	58.9	+ 25.3
Basion-prosthion	♀	45.0	50.2	54.5	62.0	+ 37.8
	♂	49.2	49.2	57.5	68.1	+ 38.4
Nasion-prosthion	♀	24.7	27.8	30.0	31.9	+ 29.1
	♂	27.3	27.6	31.1	34.5	+ 26.4
Bizygomatic breadth	♀	46.3	51.2	54.4	60.1	+ 29.8
	♂	49.2	50.0	56.7	66.3	+ 34.7
Biorbital breadth	♀	40.0	43.6	45.3	52.5	+ 31.2
	♂	42.2	43.4	47.7	56.7	+ 34.3

Measurement	Sex	Infants 3 ♀ 4 ♂	Juven. I 5 ♀ 5 ♂	Juven. II 9 ♀ 12 ♂	Adults 45 ♀ 49 ♂	% Change
Postorbital breadth	♀	38.0	39.5	39.8	40.0	+ 5.3
	♂	39.0	39.8	40.8	41.2	+ 5.6
Interorbital breadth	♀	4.3	4.0	4.6	4.9	+ 13.9
	♂	4.2	4.6	4.5	5.7	+ 35.7
Orbital height	♀	17.3	19.4	18.9	20.0	+ 15.6
	♂	18.2	18.8	19.9	19.8	+ 8.8
Palatine length	♀	21.7	25.4	29.5	33.1	+ 52.5
	♂	25.0	25.2	31.2	35.0	+ 40.0
Palatine breadth	♀	25.3	27.0	28.9	30.1	+ 19.0
	♂	26.5	27.4	29.3	31.7	+ 19.6
Postcanine length	♀	9.3	14.6	18.9	21.5	+131.3
	♂	10.7	15.8	19.7	22.0	+105.6
Mandibular length	♀	37.3	44.6	49.0	55.9	+ 49.8
	♂	43.2	43.0	51.4	61.9	+ 43.3
Average of % changes	♀	-	-	-	-	+ 30.0
	♂	-	-	-	-	+ 28.3

TABLE 21

Averages of some measurements at different ages and the total age change of these measurements, expressed as percentage of the averages for infants, in *Ateles geoffroyi* of Panama, Nicaragua and Mexico (these three series have here been combined to obtain sufficient young specimens).

Measurement	Sex	Infants 5 ♀ 4 ♂	Juven. I 4 ♀ 4 ♂	Juven. II 12 ♀ 19 ♂	Adults 116 ♀ 70 ♂	% Change
Length	♀	71.8	77.2	80.1	84.4	+ 17.5
	♂	73.7	78.8	80.3	85.2	+ 15.6
Breadth	♀	56.0	60.0	60.1	58.6	+ 4.6
	♂	58.0	59.8	60.4	58.4	+ 0.7
Height	♀	45.4	48.0	49.3	51.0	+ 12.3
	♂	47.0	51.0	50.7	51.3	+ 9.1
Basal length	♀	43.6	50.5	54.2	61.4	+ 40.8
	♂	46.0	51.2	54.5	61.7	+ 34.1
Basion-prosthion	♀	46.6	55.5	61.9	75.2	+ 61.4
	♂	49.0	55.8	62.8	75.3	+ 53.7
Nasion-prosthion	♀	22.6	27.7	31.3	37.0	+ 63.7
	♂	23.8	27.0	31.5	37.0	+ 55.5
Bizygomatic breadth	♀	42.0	51.2	55.7	65.8	+ 56.7
	♂	45.0	51.3	56.8	68.1	+ 51.3
Biorbital breadth	♀	42.0	48.0	51.1	58.3	+ 38.8
	♂	43.3	46.5	51.3	58.8	+ 35.8

Measurement	Sex	Infants 5 ♀ 4 ♂	Juven. I 4 ♀ 4 ♂	Juven. II 12 ♀ 19 ♂	Adults 116 ♀ 70 ♂	% Change
Postorbital breadth	♀	41.4	44.2	45.3	47.6	+ 15.0
	♂	42.5	44.2	45.8	47.8	+ 12.5
Interorbital breadth	♀	5.9	6.7	7.0	8.8	+ 49.2
	♂	5.8	6.0	7.1	9.0	+ 72.3
Orbital height	♀	17.0	19.3	20.8	22.3	+ 31.2
	♂	18.2	20.2	20.5	22.1	+ 21.4
Palatine length	♀	21.4	26.5	30.9	36.5	+ 70.5
	♂	22.7	26.7	32.3	36.9	+ 62.5
Palatine breadth	♀	23.2	27.7	28.9	31.5	+ 35.7
	♂	24.5	27.5	29.1	31.5	+ 28.5
Postcanine length	♀	9.9	14.7	19.4	23.2	+134.3
	♂	10.2	15.0	19.7	22.8	+123.5
Mandibular length	♀	37.6	48.5	54.6	67.2	+ 78.7
	♂	40.7	48.3	56.2	67.5	+ 65.8
Average of % changes	♀	-	-	-	-	+ 47.4
	♂	-	-	-	-	+ 42.8

TABLE 22

Averages of the same measurements as in the Tables 19 to 21 in infantile and adult *chimpanzees* and *men* and the age change in these measurements, expressed as percentage of the averages for infants.

Measurement	Sex	Chimpanzee			Man			Measurement	Sex	Chimpanzee			Man		
		Infants 7 ♀ 10 ♂	Adults 25 ♀ 25 ♂	% Change	Infants 7 ♀ 7 ♂	Adults 21 ♀ 21 ♂	% Change			Infants 7 ♀ 10 ♂	Adults 25 ♀ 25 ♂	% Change	Infants 7 ♀ 7 ♂	Adults 21 ♀ 21 ♂	% Change
Length	♀	109.6	133.1	+ 21.4	150.1	178.0	+ 18.6	Postorbital breadth	♀	66.7	71.0	+ 6.4	80.1	94.3	+ 17.7
	♂	112.8	137.2	+ 21.6	159.0	185.5	+ 16.7		♂	68.0	70.2	+ 3.2	84.6	95.9	+ 13.4
Breadth	♀	92.1	100.0	+ 8.6	120.3	133.2	+ 10.7	Interorbital breadth	♀	10.1	20.3	+ 101.0	18.6	25.6	+ 37.6
	♂	94.3	103.0	+ 9.2	131.3	139.3	+ 6.1		♂	10.8	21.2	+ 96.4	19.4	25.5	+ 31.4
Height	♀	75.4	81.6	+ 8.2	112.3	129.0	+ 14.9	Orbital height	♀	29.9	33.8	+ 13.0	30.6	34.6	+ 13.1
	♂	77.7	85.3	+ 9.8	118.8	133.9	+ 12.7		♂	30.7	33.6	+ 9.4	31.8	34.7	+ 9.1
Basal length	♀	70.1	98.8	+ 40.9	75.0	97.3	+ 29.7	Palatine length	♀	40.4	72.5	+ 79.4	33.1	52.6	+ 58.9
	♂	69.5	99.9	+ 43.7	81.4	103.7	+ 27.4		♂	41.3	75.4	+ 82.5	35.3	53.6	+ 51.8
Basion-prosthion	♀	78.0	133.9	+ 71.6	69.3	96.1	+ 38.7	Palatine breadth	♀	42.3	61.2	+ 44.6	47.1	61.1	+ 29.7
	♂	79.9	138.6	+ 73.4	76.1	100.4	+ 31.9		♂	44.2	63.0	+ 42.5	49.4	63.0	+ 27.5
Nasion-prosthion	♀	51.9	84.7	+ 63.1	43.7	66.8	+ 52.8	Postcanine length	♀	14.9	43.4	+ 191.2	16.3	40.2	+ 146.5
	♂	54.8	88.8	+ 62.0	50.3	71.6	+ 42.3		♂	15.4	44.8	+ 190.9	17.0	38.7	+ 127.5
Bizygomatic breadth	♀	79.4	120.7	+ 52.0	91.3	123.4	+ 35.1	Mandibular length	♀	71.9	126.3	+ 75.6	66.1	95.7	+ 44.7
	♂	83.9	132.4	+ 57.8	99.0	130.8	+ 32.1		♂	74.6	132.5	+ 77.6	70.7	99.6	+ 40.9
Biorbital breadth	♀	70.9	104.2	+ 46.9	83.1	108.4	+ 30.4	Average of % changes	♀	-	-	+ 54.9	-	-	+ 38.6
	♂	72.0	108.5	+ 50.7	88.6	112.0	+ 26.4		♂	-	-	+ 55.4	-	-	+ 33.1

N.B. All infants have full first dentition and all adults have had completed the eruption of their permanent teeth, though in some cases a few of the latter teeth had become lost later on and in 4 men the M3 are congenitally lacking. The series for adult man are composed of 3 times as many skulls of each race and sex as in the series for infantile man.

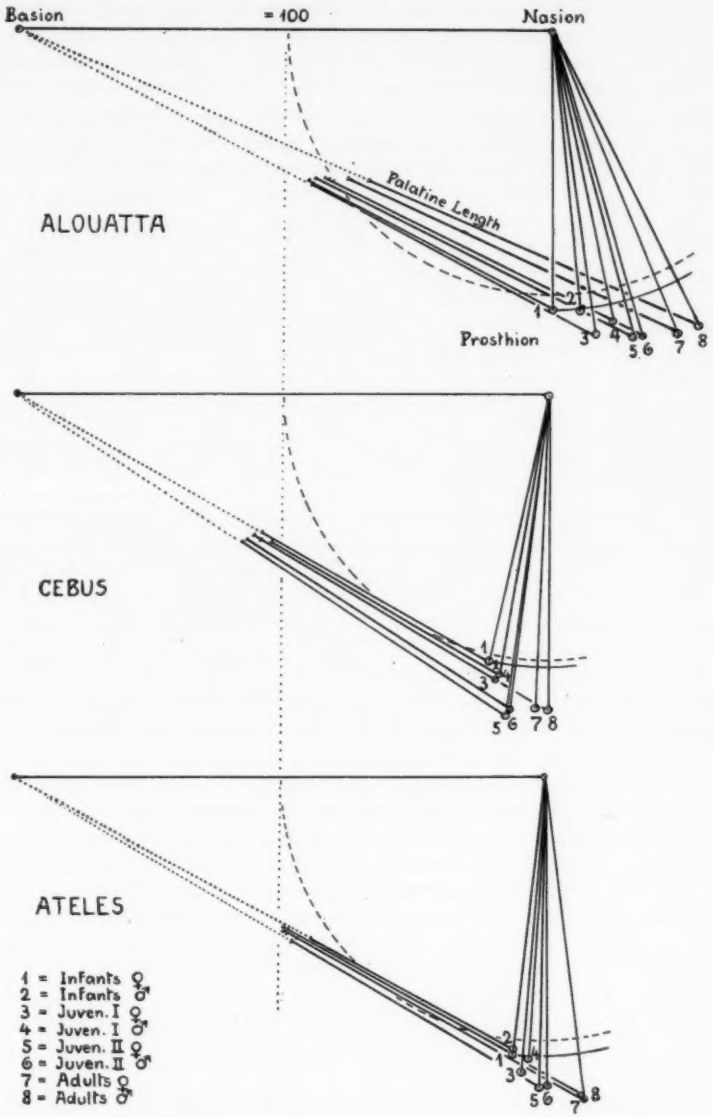

Fig. 3.—The postinfantile age changes in the triangle nasion-basion-prosthion and the palatine length constructed from the relevant average measurements after these had been calculated in percentage of the corresponding nasion-basion distances. The data, used for this figure, are the same as in the Tables 19 to 21.

The bizygomatic and biorbital breadths show the greatest relative age changes in *Alouatta* and the smallest in *Cebus*. In *Alouatta* the relative increments of these measurements are even much larger in males than in females, in *Cebus* they are nearly alike in both sexes and in *Ateles* they are actually smaller in males. The neurocranial postorbital breadth grows comparatively little after birth, especially in those primates in which the orbits gradually move forward and thereby leave a postorbital constriction.* It is only in those exceptional primates, in which the orbits remain fully underneath the brain case, like *Ateles* and *Homo sapiens*†, that this frontal breadth of the neurocranium increases about as much as the cranial length. The relative postinfantile increase of the interorbital breadth is very marked in *Alouatta*, *Ateles* and chimpanzee, but comparatively modest in *Cebus* and in man. Among the platyrrhines this diameter grows more intensively in males than in females. The reasons for these marked differences are as yet unknown since the existence and development of ethmoidal cells can at best play only a partial role. The percentage age changes in the orbital height are rather small in all these series, unquestionably because the eyes and orbits grow much more rapidly before than after infantile life in all primates, as has been demonstrated in another publication by the writer (1940).

The remaining four measurements in the Tables 19 to 22 appertain to the masticatory apparatus which increases in size most intensively during postinfantile life. In every instance the palate changes much more in length than in breadth and the relative change in mandibular length corresponds closely to that in palatine length, as is to be expected††. By far the greatest postinfantile change takes place in the postcanine length, which increases always by more than 100 per cent of its initial size. It is rather surprising that these two palatine and one dental measurements show a relatively smaller age change in *Cebus* than in man, with the mandibular length differing but little in this respect.

Of all the percentage changes in the Tables 19 to 22 those appertaining to the splanchnocranium are generally much larger than those of the neurocranium, which grows after infantile life not nearly as much as the former. The exceptions to this rule are formed by the size of the orbit and the length of the skull base which show generally intermediate degrees of relative change. The averages of these percentage changes for each species equal roughly 29 for *Cebus*, 36 for man, 45 for *Ateles*, 50 for *Alouatta*, and 55 for chimpanzee. Only in *Alouatta* is this average change clearly greater in males than in females, none of the other species having such a pronounced sex difference. These results will gain in interest when more strictly corresponding data for still other primates have become available, which the writer hopes to supply in the near future.

* In orang-utans with their extreme postnatal orbital migration the average postorbital breadth is even larger in juveniles than in adults. (Schultz, 1941).

† Several platyrrhines, besides man, retain the typically fetal position of the orbits throughout life (Schultz, 1949).

†† From Fig. 3 it is apparent that the relative position of the aboral end of the palatine length is surprisingly constant during growth in contrast to the marked changes at the oral end.

In view of the widely differing rates of change in the various cranial dimensions, it is to be expected that the proportions of the skull can also change with age very considerably. This is demonstrated here by means of two examples in Table 23. The length-breadth index decreases with age by about 10 units in all three species and the relative basal length increases by between 9 and 13 units. The direction of both these age changes corresponds to that forming the rule among all simian primates whose cranial development has been studied so far.

Considerable evidence has accumulated to show that in man some dimensions of the head continue to change with advancing age after adulthood has been reached. The present material seems suitable for studying the question, whether the skulls of monkeys do change in a correspondig manner during adult life. For a preliminary attempt to answer this question the averages of some measurements have been calculated separately for each of the three successive age groups of adults in the largest of the series ; these averages are listed in Table 24. The data demonstrate first of all that significant age changes do occur in some, but not in all, measurements. For instance, the averages of length change generally much more than those of breadth and of height and the averages of bizygomatic breadth show much more marked differences between successive age groups than do those of palatine length. The averages of age group *1* are larger than the corresponding averages of group *0* in all of the eight series in Table 24 regarding basal length, basion-prosthion, nasion-prosthion, and bizygomatic breadth, the former averages are also larger than the latter in seven out of eight instances for length and for palatine length, and only breadth and height do not show such an increase in all or a great majority of the cases. Even though this is only a crude analysis, it seems justified to conclude that many cranial dimensions do continue to increase from early to middle adult life by appreciable amounts. Since there are only very modest numbers of specimens in the age groups *2* the averages of these groups may not represent the typical conditions very closely. It may be stated, nevertheless, that the averages of the groups *2* are smaller than the corresponding averages of the groups *1* nearly twice as often as the reversed condition is found. It seems, therefore, that in old age many measurements tend to decrease slightly. The palatine length, e.g., averages less in senile specimens than in those of middle adult life in all eight series.

The distance between the temporal lines decreases with advancing age in all series and this much more in males than in females of the same local population. This is of course a clear proof that the temporal muscles continue to expand higher on the cranial vault to old age, when they can occasionally meet and even induce the development of a midsagittal crest in a few old males*.

* Midsagittal crests exist in the entire present material in only four *Alouatta* and one *Cebus*, all of which are males of the age groups **1** or **2**. In every one of these five skulls the length and breadth of the cranial vault is below average size while the palatine measurements lie at or even above their corresponding averages. None of these crests exceed 2 mm. in greatest height. Among the author's few *Cebus apella* from South America there are two old males with much larger crests, beginning right above the glabella and reaching their maximum height in the frontal region, thus differing markedly from the crest formation in *Cebus capucinus*.

TABLE 23

Averages of two cranial indices at different ages, based upon the same material as used for the Tables 19 to 21.

Age	Sex	Breadth / Length			Basal length / Length		
		Alouatta (Panama)	Cebus (Panama)	Ateles (Pan. Nic. Mex.)	Alouatta (Panama)	Cebus (Panama)	Ateles (Pan. Nic. Mex.)
Infants	♀	80.4	77.0	78.0	74.7	63.5	60.7
	♂	80.6	76.8	78.7	75.8	65.1	62.4
Juven. I	♀	77.4	73.7	77.7	77.8	67.0	65.4
	♂	76.3	75.0	76.0	79.4	65.3	64.9
Juven. II	♀	74.0	73.2	75.0	82.1	68.2	67.6
	♂	75.3	72.6	75.2	83.0	70.1	67.8
Adults	♀	71.4	69.3	69.4	86.1	72.5	72.8
	♂	69.8	67.2	68.5	89.3	74.6	72.4

TABLE 24

Changes in the averages of some cranial measurements in the three successive age groups of adults.

Series	Sex	Age Group	Specimens	Length	Breadth	Height	Basal length	Basion-prosthion	Nasion-prosthion	Bizygomatic breadth	Palatine length	Distance b. tempor.lin.
Alouatta, Panama	♀	0	51	68.2	49.2	38.5	58.4	79.4	35.9	68.9	40.2	19.7
		1	80	69.4	49.3	38.4	59.9	82.0	36.6	71.1	41.0	16.2
		2	13	70.2	49.7	38.3	60.2	82.2	37.1	73.0	40.2	16.9
	♂	0	18	72.7	51.4	38.7	64.8	90.2	40.0	78.7	44.2	14.2
		1	32	74.8	51.6	38.9	67.0	93.8	41.5	82.0	45.3	8.2
		2	7	72.1	50.9	38.9	64.7	89.7	39.9	80.0	44.0	8.4
Alouatta, Nicaragua	♀	0	16	68.6	49.3	37.4	58.1	79.2	36.5	67.6	40.9	19.4
		1	40	69.7	50.0	37.6	59.3	81.9	37.5	70.9	41.5	17.6
		2	4	68.3	49.0	37.5	58.8	80.5	36.5	70.3	40.5	17.5
	♂	0	10	73.0	52.4	37.6	63.3	90.2	40.7	78.7	45.3	14.3
		1	34	74.5	51.9	38.1	65.7	94.4	42.5	82.8	45.9	8.4
		2	6	75.3	52.3	37.7	67.2	95.2	42.0	83.5	45.5	7.0
Cebus, Panama	♀	0	15	75.2	52.8	46.1	53.9	60.9	32.0	59.5	33.3	31.9
		1	26	75.3	51.7	45.6	54.8	62.7	32.1	60.3	33.3	26.5
		2	4	74.3	51.7	45.5	54.5	61.5	29.8	60.7	32.0	25.0
	♂	0	22	78.2	53.2	47.2	57.4	66.2	33.7	63.7	34.7	24.5
		1	24	79.9	53.0	47.2	60.2	69.7	35.3	68.7	35.2	12.8
		2	3	78.3	52.0	45.3	60.0	69.0	35.0	67.3	35.0	8.3
Ateles, Panama	♀	0	26	83.8	59.7	50.5	60.5	73.9	36.4	65.4	36.6	41.8
		1	34	85.9	58.5	50.9	62.5	77.3	37.9	68.3	37.5	38.6
		2	3	88.7	60.7	52.3	63.0	76.0	36.0	70.0	35.7	36.7
	♂	0	11	86.3	60.3	50.5	61.2	74.5	37.5	67.8	37.4	39.0
		1	16	85.3	57.6	50.4	62.9	77.8	38.2	70.8	37.5	29.1
		2	3	87.7	58.7	50.3	64.0	77.0	39.7	71.0	37.3	30.7

SUTURES AND FONTANELLAR BONES

As has recently been demonstrated by Chopra (1957), the cranial sutures of most platyrrhines generally remain open for a comparatively longer period of life than in other simian primates and certainly much longer than in the anthropoid apes. Since Chopra has already given a detailed account of suture closure in monkeys, including the three genera of this report, it suffices to discuss here merely the sequence of obliteration of some few sutures, selected for their special interest. For this purpose the entire material of each species could be combined, since neither racial nor sexual differences seem to exist in the age changes of sutures. In infantile skulls the sutures are as yet always fairly simple lines without any marked denticulations. In most cases this uncomplicated sutural form is retained with little change to adult life, but in some older juvenile or adult skulls the vault sutures can become highly complicated by forming innumerable small processes. These striking and as yet totally unexplained differences in the detailed form of sutures are particularly common among adult *Ateles*.

The first postnatal fusions between cranial elements take place at the interfrontal or metopic suture, between the parts of the occipital bone and between the mandibular halves at the symphysis. From the relevant data in Table 25 it is seen that the metopic suture begins to disappear before the deciduous dentition has become completed, but can remain partly open in a minority of cases in *Alouatta* and in *Ateles* until the first stages of juvenile life, whereas in *Cebus* it is obliterated completely in all specimens with full first dentition. In the available material it was invariably the lowest part of the metopic suture which was the last to close.

The occipital elements do not become united until the beginning of the juvenile period and then more rapidly in *Alouatta* than in *Cebus* and even somewhat later in *Ateles*. Among the latter two the lateral occipitals fuse with the basi-occipital slightly sooner than with the occipital squama, but in *Alouatta* this relation is usually reversed.

The mandibular symphysis, which remains open permanently in most prosimians, becomes obliterated in *Cebus* by the time the first dentition has been completed, but in *Alouatta* and *Ateles* not until at least some permanent teeth have erupted. This fusion of the mandibular halves begins always lingually and takes place last on the labial side of the alveolar border.

From the data in Table 26 it is apparent that the main sutures of the neurocranium all tend to close much earlier in adult life in *Alouatta* than in *Cebus* and *Ateles*. Among the latter the three main sutures of the vault are still partly or even fully open in the great majority of the specimens of the oldest age group, whereas in *Alouatta* these sutures have already become fully closed in from 12 to 19 per cent of the cases in the youngest age group. Even the basilary suture disappears sooner in *Alouatta* than in the other two species. The internasal suture, in contrast to the former sutures, remains open longest in *Alouatta*, being still entirely open in more than one-fourth of even the oldest specimens. *Cebus* differs markedly from the other two species by the early obliteration of its intermaxillary sutures (the facial, but not the palatine parts).

TABLE 25

The percentage occurrence of partly and of fully obliterated metopic sutures and of partly and fully fused occipital elements and mandibular halves in infantile and the younger juvenile skulls. I=infants with incomplete first dentition, II=infants with complete first dentition, III=juveniles with only first permanent molars, IV=juveniles with at least some permanent incisors and second molars, but no other permanent teeth. n=number of specimens.

Feature	Age / Fusion / n	Alouatta				Cebus				Ateles			
		I	II	III	IV	I	II	III	IV	I	II	III	IV
	n	3	24	27	29	5	8	9	12	0	9	7	9
Metopic suture	partly	100	25	4	0	40	0	0	0	-	44	29	22
	fully	0	75	96	100	20	100	100	100	-	56	71	78
Occipital elements	partly	0	21	22	0	0	0	69	42	-	0	57	89
	fully	0	0	70	100	0	0	11	58	-	0	0	11
Mandibular halves	partly	33	96	74	14	40	0	0	0	-	100	43	22
	fully	0	0	26	86	20	100	100	100	-	0	57	78

TABLE 26

The percentage occurrence of partly and of fully closed sutures among the *adult* skulls of all series separated into the three successive age groups. n=numbers of specimens.

Suture	Age / Closure / n	378 Alouatta			118 Cebus			203 Ateles		
		0	1	2	0	1	2	0	1	2
	n	123	219	36	49	61	8	72	110	21
Basilary	partly	6	0	0	6	7	12	6	0	0
	fully	41	100	100	10	90	88	12	100	100
Coronal	partly	15	5	0	0	15	50	1	11	43
	fully	19	95	100	0	0	25	0	4	14
Sagittal	partly	10	11	3	0	5	50	0	1	0
	fully	12	84	97	0	5	12	0	3	24
Lambdoid	partly	13	9	0	0	8	37	0	3	24
	fully	14	88	100	0	3	12	0	1	19
Internasal	partly	0	18	33	14	10	12	6	24	5
	fully	0	2	39	37	84	88	6	46	95
Intermax.-max.(fac.)	partly	14	16	0	31	0	0	7	27	14
	fully	6	80	100	69	100	100	7	39	86

While recording the conditions of the sutures in the entire material a surprisingly high number of cases was encountered with clearly abnormal suture closure, namely the following : The coronal suture of one side only had become prematurely closed and the corresponding half of the cranial vault had been retarded in its growth in all together twelve adult skulls, of which three are

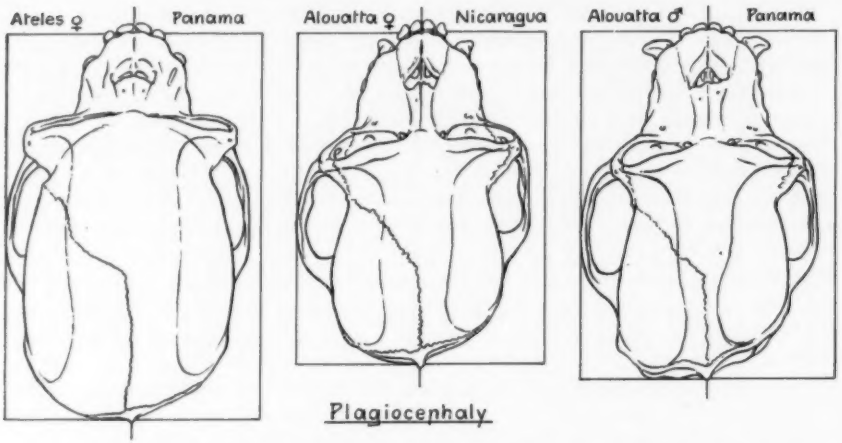

Fig. 4.—Exact vertical views of three adult skulls with plagiocephaly showing the premature obliteration of the coronal suture on one side and the retarded growth of the neurocranium on the corresponding side.

shown in Fig. 4. Three of these plagiocephalic specimens are *Ateles* (2 females, 1 male) and the other nine are all *Alouatta* (8 females, 1 male). The frequency of this condition amounts to 2·4 per cent among the adult *Alouatta* and to 1·5 per cent among the adult *Ateles*. The *Cebus* series contained not a single case of plagiocephaly, but one of so-called scaphocephaly in which the sagittal suture had become fully closed in a juvenile I specimen. Among the *Alouatta* there is also an exactly corresponding case of scaphocephaly in a juvenile II. Of other sutural abnormalities the following are noteworthy : In one *Ateles* the left parietal is divided in two parts by an abnormal central, roughly horizontal suture and the right parietal shows a corresponding, but incomplete suture. In another *Ateles* and in one *Cebus* there exist very similar marginal clefts or incomplete sutures in the parietals. Also in one adult *Ateles* and one adult *Cebus* the right alisphenoid is completely divided by an abnormal horizontal suture. In the entire material of *Alouatta* not a single case of this sort could be found.

The frontal bone of *Cebus* and of *Ateles* normally reaches far back between the parietals and, particularly in the former, the aboral, central part of the frontal can take the form of a long and narrow process, as in the examples 1 and 2 in Fig. 5. In place of such processes there occur frequently separate bones which have closed the great fontanelle of fetal life and which can continue

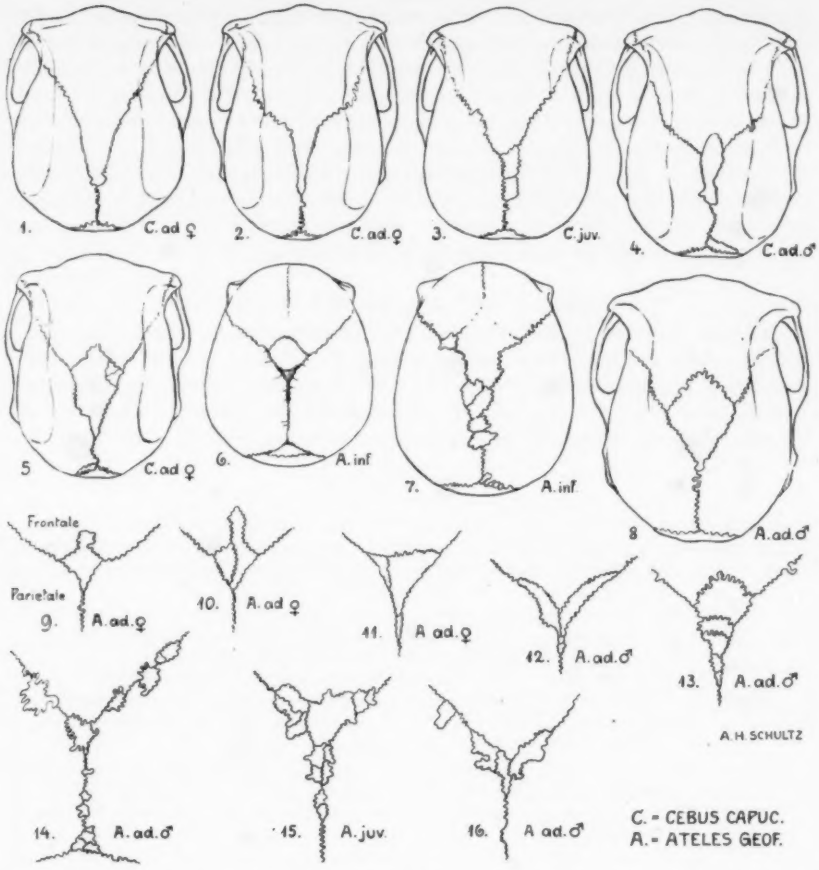

Fig. 5.—Sketches of extremely long interparietal processes of the frontal bone (1 & 2) and of bregmatic (3 to 16), lambdoid (4, 5, 6 & 14) and sutural (14 & 15) bones in *Cebus* (1 to 5) and *Ateles* (6 to 16).

along the adjacent sutures, as is illustrated by the sketches in Fig. 5. These so-called bregmatic fontanelle bones exist among the 251 *Ateles* of the present material in 105 cases, or with a frequency of 42 per cent, among the 167 *Cebus* in 26 cases, or in 16 per cent, but among the 493 *Alouatta* in only one infantile specimen (=0·2 per cent). Bregmatic fontanelle bones were present in 12 per cent of the cases in a series of *Colobus badius*, whereas in not a single skull of a large series of *Colobus polykomos* and they existed in 15 per cent of *Hylobates lar*, but not in any *Hylobates moloch* according to other studies by the writer (1944, 1958). These facts indicate clearly that there must be a hereditary basis for the occurrence of such bones (see also Schultz, 1923). This

conclusion is supported also by the finding that among our *Ateles* these fontanelle bones are nearly twice as frequent in the Guatemalan and Mexican series as in the Panamanian and Nicaraguan series and while the latter contained only specimens with single (42 cases), double (seven cases) and triple (one case) bones, in the former series there are besides single (29 cases), double (seven cases) and triple (seven cases) bones cases with anywhere from four to ten bones (seven cases). Lambdoid fontanelle bones are much rarer than bregmatic ones, but also more frequent in *Ateles* (=11 per cent) than in *Cebus* (=3 per cent) and totally absent in *Alouatta*. Both these types of fontanellar bones do occur practically as often in males as in females.

VARIATIONS IN SOME SPECIAL CRANIAL FEATURES

That some cranial characters are much more variable in most monkeys than in man is exemplified by the number of infraorbital foramina. This number (per side) varies in the present material between one and seven, as shown by Table 27. A single infraorbital foramen, which exists in over 90 per cent of human skulls, is comparatively rare among platyrrhines.

TABLE 27

Percentage frequencies and averages of the number of infraorbital foramina per side. Since these numbers differ on the right and left very frequently the percentages have been calculated for the totals of sides. There are no significant differences in the local series of *Cebus*, hence they are not listed separately.

Genus	Series	Sides	Number of Foramina							
			1	2	3	4	5	6	7	Aver.
Alouatta	Panama	530	51	42	6	1	-	-	-	1.57
	Costa Rica	30	80	20	-	-	-	-	-	1.20
	Nicaragua	300	62	31	7	0.3	-	-	-	1.45
	Guatemala	46	2	46	39	7	2	2	2	2.76
	Mexico	80	5	38	36	20	1	-	-	2.75
Cebus	all series	334	0.6	10	49	34	6	0.3	-	3.37
Ateles	Panama	236	0.5	26	48	22	3	-	-	3.00
	Costa Rica	22	-	18	59	18	5	-	-	3.09
	Nicaragua	96	-	20	51	24	5	-	-	3.15
	Guatemala	12	-	17	8	50	17	8	-	3.92
	Mexico	136	-	14	36	29	13	7	0.7	3.63

Multiple foramina are more common in *Cebus* and *Ateles* than in *Alouatta*, but among the latter they are clearly more frequent in the Guatemalan and Mexican series than in the other and more southern series. Curiously enough, a corresponding difference is found between the local series of *Ateles* among which also the two northernmost series have the highest average numbers. That the number of infraorbital foramina must be genetically determined is evident not only from such marked species differences, as the writer (1958) has found among Liberian *Colobus*, but also from the above-mentioned differences between local populations of one and the same species. A very similar difference exists also between the northern and the southern *Hylobates lar* (Schultz, 1954).

The number of foramina mentalia in each mandibular half varies in the platyrrhines under investigation between 1 and 5. As shown by Table 28, *Ateles* tends to have fewer such foramina than *Cebus* and *Alouatta* which possess multiple foramina in the majority of the cases. In *Ateles*, as also in *Colobus*, single foramina represent the rule. Neither the number of infraorbital nor that of the mental foramina differs significantly and consistently according to sex or side in any of these platyrrhines.

TABLE 28

Percentage frequencies and averages of the number of foramina mentalia per side. The local series are not listed separately since they do not differ significantly.

Genus	Sides	Number of Foramina					
		1	2	3	4	5	Aver.
Alouatta	986	42	38	17	3	0.5	1.82
Cebus	334	26	51	19	3	0.6	2.01
Ateles	502	78	19	3	-	-	1.25

A foramen zygomatico-orbitale has been retained in all platyrrhines as a remnant of the original communication between orbit and temporal fossa. As a rule this foramen is very small, but in *Ateles* its size varies in an unusual degree, as shown by the examples in Plate 1 and in Fig. 2. Foramina, even larger than that in the lower skull of Fig. 2, have been encountered in several adult *Ateles geoffroyi*, yet in others from the same locality there were only minute openings, barely permitting the passage of a hair. In *Alouatta* and in *Cebus* these foramina are invariably small.

A cranio-pharyngeal canal, penetrating the basisphenoid, is a normal embryonic feature which can persist to adult life among primates with highly variable percentage frequencies. In man, e.g. this canal has remained fully open in only about 0·5 per cent of adults, in gibbons in 30 per cent, and in chimpanzees in 74 per cent (Schultz, 1944) In the present material a cranio-pharyngeal canal was noted in 16 per cent of the *Ateles*, in only 0·8 per cent

of the *Alouatta* and in not a single case of *Cebus*. In the former two species the canal was somewhat more frequent among the younger than the older specimens.

Some topographic features of the skull can also vary extensively in these platyrrhines. For instance, in all our *Alouatta* the lacrimals meet the nasals with only two exceptions in which the maxillaries had grown all the way to the frontal, thus separating the former two bones. In the *Cebus* series, on the other hand, the lacrimals lie well within the orbit and do not reach the nasals in all but three of the skulls, the latter having unusually short frontal processes of the maxillaries, combined with quite broad nasal bones which actually make contact with the lacrimals. *Ateles* represents in this respect an intermediate stage, since in roughly two-thirds of the cases the lacrimals and nasals do touch each other, whereas in the remaining cases the maxillaries send narrow arms to the frontal, thus wedging the former two bones apart. It may be mentioned here also that, according to Serra and Picosse (1952), in *Callithrix* a fronto-maxillary suture exists in roughly two-thirds of the specimens, the others having naso-lacrimal sutures.

AGE CHANGES IN THE DENTITION

The sequence of eruption of the deciduous teeth has so far become known for only few primates and these are all catarrhines. The present material of *Alouatta* and of *Cebus* contains some infants, with as yet incomplete first dentitions* which permit the following tentative statements in regard to the order of appearance of the milk teeth above their alveoli : In both species the incisors are unquestionably the first to erupt, to be followed by the first molars (the lower ones slightly before the upper ones). In *Alouatta* the second milk molars follow the first ones, but in *Cebus* the canines have appeared before the second molars in the only specimen available for this stage of development. In two other *Cebus* the canines are fully out while only the lower of the third molars have partly erupted. In *Alouatta* the eruption of the canines and third molars occurs last and in rapid and probably variable order. The formulae for these sequences can tentatively be written as follows :

Alouatta = i1 — i2 — m1 — m2 — (c m3)

Cebus = i1 — i2 — m1 — c — m2 — m3

If, naturally, m3 is disregarded, the formula for *Cebus* is identical with that for Old World monkeys, gibbons and man, whereas the formula for *Alouatta* corresponds to that of the great apes which are also characterized by the late eruption of the canines (Schultz, 1944 and 1956 a).

The eruption of the permanent teeth does not begin until after a considerable period of rest following upon the completion of the first dentition, as seems highly probable from the fact that specimens with full sets of deciduous teeth are much more numerous than those with either still incomplete first dentitions or those with the first added one or two permanent teeth. The order of

* A few additional skulls of early infantile *A. palliata* and of *C. capucinus* could be utilized for this purpose, though not for others since they were damaged or incomplete, except for their dentitions. Unfortunately there were no early infants of *Ateles* available for this study.

eruption of the permanent teeth in the three platyrrhine genera, with which the present report is concerned, had already been studied by the writer in 1935 and again by Serra in 1952. The extensive material on which both these publications had been based contained different species for each of the genera, whereas the present series are all composed of only one species for each genus and hence justify a new analysis of the sequence of eruption, free from possible species differences. It can be stated at once that not only had Serra fully confirmed the previous relevant findings of the writer, but that the new results, based upon the present material, also agree in every essential detail with the preceding conclusions. The order of eruption* of the permanent teeth is in general the same for *Alouatta* as for *Cebus* and for *Ateles* and can be most briefly represented by the following formula :

M1 — I1 12 M2 — (P1 P2 P3) — C M3

The parentheses indicate that the premolars tend to appear in rapid and variable sequence, though most often in the order given above, and the horizontal lines mark clear intervals in the process of eruption, as seems most likely from the relative frequency of specimens with the particular formulae attained just before these intervals. The mandibular teeth erupt as a rule well before the corresponding maxillary ones, so that occasionally the lower M2 can appear even before the upper I2 and the lower M3 before the upper C. It should be specially mentioned here that this sequence of " appearance " is not necessarily the same as the sequence of finished eruption or occlusion which differs particularly in regard to the canines and last molars of males. In many of the latter the large canines are not yet fully out when the M3 have reached the plane of occlusion. In some prosimians and in *Aotus* all permanent molars are added to the first dentition before the latter becomes replaced. This original order has become altered in various degrees among other primates and this always with the same tendency to accelerate the replacement of deciduous teeth, a tendency which has reached its extreme only in modern man. In the three types of platyrrhines, studied here, the shift in the sequence of eruption has gone as far as in the majority of Old World monkeys and as in all apes and also represents the highest degree of specialization in this condition among all non-human primates (Schultz, 1956 a).

In the dentition of the present, wild platyrrhines there exists normally perfect and uniform occlusion with the exception of the incisors which vary extensively in regard to the exact relation between the upper and lower teeth, as shown by Table 29. Among all our *Alouatta* there are only two cases of overbite, whereas in *Cebus* and *in Ateles* this type of occlusion is very common but underbite very rare. While in *Cebus* the frequency of overbite decreases in general with age, it increases in *Ateles*, except in the oldest specimens. Similar age changes in the relative frequency of these types of occlusion have been found also in proboscis monkeys, gibbons, chimpanzees and gorillas (Schultz, 1956 a). The high frequency of underbite is not limited to *Alouatta palliata*, but has been found also in various other species of this genus by

* By " eruption " is here meant the beginning appearance of the crown *above* the alveolar border in the skull. As soon as a permanent tooth has also pierced the gum it becomes partly discoloured in all these monkeys.

TABLE 29

Percentage frequencies of the three main types of occlusion of the incisors at different ages. All local series and both sexes of each species combined. Numbers of specimens as in Table 1.

Genus	Age	Underbite	Edge to edge	Overbite
Alouatta	infantile	67	33	0
	juvenile	50	50	0
	adult 0	49	49	2
	adult 1	49	51	0
	adult 2	47	53	0
Cebus	infantile	0	38	62
	juvenile	0	25	75
	adult 0	0	43	57
	adult 1	3	67	30
	adult 2	13	87	0
Ateles	infantile	0	75	25
	juvenile	3	62	35
	adult 0	1	36	63
	adult 1	0	32	68
	adult 2	5	52	43

Serra (1951). Besides in *Alouatta* underbite is common in only few other primates, notably in *Colobus* and in *Nasalis* (Schultz, 1942, 1958). It is to be mentioned also that among adults the characteristic underbite of *Alouatta* is somewhat more frequent in males than in females and that overbite in adult *Cebus* and *Ateles* is slightly less frequent in males than in females. In many of the adult female *Alouatta* with underbite the diastemata between the upper C and I_2 are very narrow or even totally lacking, though there are also other cases of underbite associated with diastemata of average width.

ABNORMAL AND DISEASED CONDITIONS OF THE SKULL AND TEETH

The frequent cranial abnormalities, consisting of fontanellar bones and accessory and prematurely closed sutures, have already been enumerated. Surprisingly few other developmental abnormalities have been encountered

among the more than 900 skulls in the present series. In one adult female *Alouatta* the left postglenoid process is strikingly stunted, having less than one-fourth the size of the normal, right one. In three other adult *Alouatta* the sagittal axis of the face part does not coincide with that of the brainpart, but is markedly bent toward the right side. In two of these cases this asymmetry is evidently connected with the congenital lack of the right upper P_1, but the third and equally pronounced case is not accompanied by any other asymmetries in either its sutures or its teeth.

The following clearly pathological conditions have been found among these skulls of wild-shot specimens : (A) More or less well repaired fractures exist in fifteen *Alouatta* (9 ad. males, 5 ad. females, 1 juv. female) six times on a zygomatic arch, five times on the mandible and four times on the supra-orbital rim, in four *Cebus* (4 ad. males), twice on a zygomatic arch and twice on the mandible, and in three *Ateles* (3 ad. males) three times on the mandible. With one exception all these mandibular fractures had occurred on the ramus. It can hardly be regarded as a mere chance that the great majority of these cases are males and all but one are adults and even mostly belonging to the age group **2**. (B) Clear signs of infections appertain chiefly to sinuses (besides the numerous alveolar abscesses to be discussed below). In one adult *Alouatta* and one adult *Ateles* there are large drainage holes leading from one maxillary sinus into the nasal cavity, the orbit and the temporal fossa and in five adult *Cebus* one or both frontal sinuses have become exposed by irregularly shaped and situated holes with evidently partly healed borders. In two juvenile *Alouatta* the centre of the hard palate bears a circular large area of thickened and porous bone with some fine perforations leading into the nasal cavity, apparently due to some local infection. (C) Arthritic changes were found in the temporo-mandibular joints of one *Alouatta*, five *Cebus* and one *Ateles*, all fairly or very old animals. These changes consist of marked enlargement and flattening of the mandibular condyles and the glenoid fossae through exostoses accompanied by pitting and other irregularities of the joint surfaces. In three of these cases both mandibular joints are affected, in the remaining four cases only one joint. In a survey of the occurrence of pathological conditions among primates the writer (1956 b) had reached the conclusion that arthritis seems to be restricted to catarrhines. This can no longer be maintained in view of the just mentioned new cases of platyrrhines which show changes identical with those found in catarrhines, though not as extreme as in some of the latter. In *Alouatta* and *Ateles* arthritis is evidently very rare, but not in *Cebus*, among which it has now been found in five out of sixty-nine specimens of the age groups **1** and **2**.

Developmental abnormalities of the teeth are surprisingly common in these Central American monkeys, particularly in the second dentition. The distribution and relative frequencies of these abnormalities leave no doubt that most of them must have a genetic basis and rarely occur at random anywhere in the dentition. Supernumerary teeth are represented by only five cases, namely by lower fourth molars on both sides in one *Ateles*, on one side only in another *Ateles* and an *Alouatta*, and by one extra upper and one extra lower premolar in two *Alouatta*, both from Guatemala (see Fig. 6, Nos. 11 &

12). Congenital lack of teeth is far more frequent, having been found in the following specimens: lack of two upper and all four lower I with partial retention of i in one *Alouatta* (Fig. 6, No. 6), lack of one upper I2 in two other *Alouatta* and lack of both lower I1 in two and of only one lower I1 in thirteen *Alouatta*. All these eighteen *Alouatta* are adult. Among three additional adult *Alouatta* the upper I2 have been recorded as vestigial once and the lower

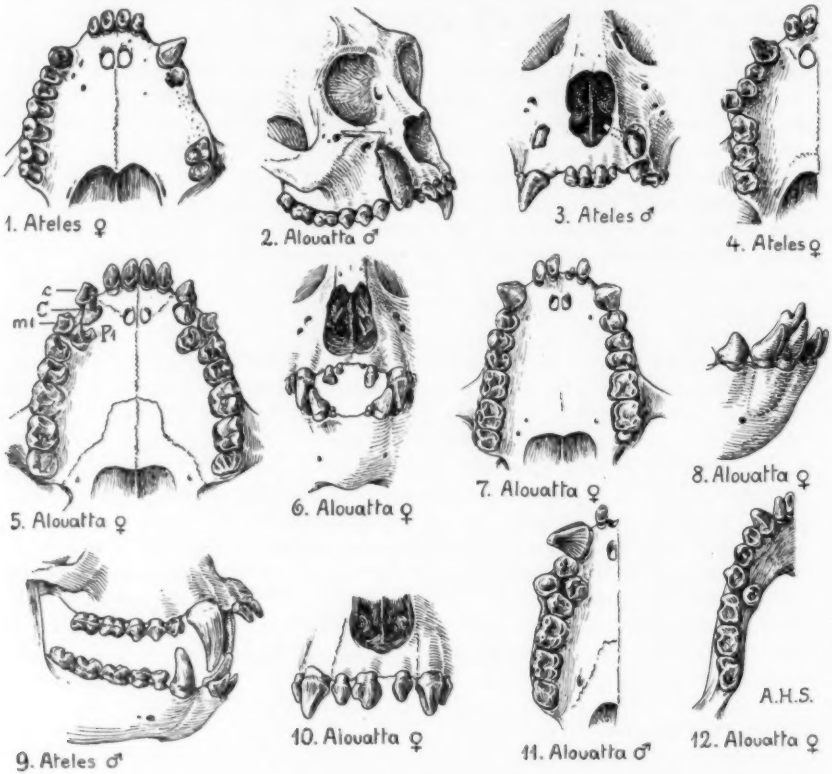

Fig. 6.—Sketches of dentitions of adult Central American *Alouatta* and *Ateles* showing pathological and teratological conditions. 1. = extensive wear, abscess formation and loss of teeth in a senile specimen. 2. = destruction of alveolar wall of broken and infected r. C. 3. = abscesses on both C with l.C. impacted, stunted and with abnormal branch of the root reaching into nasal cavity. 4. = r. P 3 crowded labially. 5. = both C and P 1 crowded lingually with retention of both c and m 1. 6. = both upper I 1 and all lower I congenitally lacking and retention of both upper i 1 and lower i 2. 7. = l. M 3 vestigial. 8. = malformed r. C with crown incompletely divided into four parts, but root with mere indication of a partial division. 9. = congenital lack of both upper M 3 and of lower r. P 1 and with lower r. C occluding *behind* upper C. 10. = congenital lack of upper l. I 1 and incompletely doubled r. I 1. 11. = r. P 2 crowded lingually and rotated due to supernumerary cone-shaped tooth. 12. = supernumerary misplaced tooth, resembling a P.

I1 twice. Among all our *Cebus* there is not a single instance of congenitally lacking or vestigial incisors and among the *Ateles* there is only one skull, lacking the left lower I 1 and having no space for it.

The upper first premolar is congenitally lacking on one side in two *Alouatta* and the lower first premolar of one side in one specimen of each of the three species (the case of *Ateles* is shown in Fig. 6, No. 9 ; in the case of the adult *Cebus* the corresponding m_1 is retained in place of the missing P 1).

The third molars have failed to develop in the upper jaws of two adult female Panamanian *Alouatta*, once bilaterally and once unilaterally. Among adult *Ateles* the upper M 3 are missing on both sides in five Nicaraguan specimens and on one side only in another Nicaraguan as well as in three Panamanian specimens. In *Cebus* the lower M 3 are lacking on both sides in three Panamanian adults. That these incidences of total suppression of third molars are the extremes of a more prevalent trend to reduce these teeth is evident from the numerous additional cases of vestigial M 3, of which one is shown in Fig. 6, No. 7. Such clearly degenerate last molars exist in the upper jaws of five adult *Alouatta* (four times bilaterally) and of thirteen adult *Ateles* (seven from Nicaragua and six from Panama). In *Cebus* all four M 3 are markedly reduced in three adults and only the upper M 3 in fourteen other adults. These exceptionally high frequencies of reduced and lacking last molars in at least our three species of Cebidae, among which the other molars never showed any noteworthy variations, are of special interest in view of the fact that in the other platyrrhine family, the Callithricidae, the third molars have become totally eliminated with the exception of *Callimico*.

Besides the just mentioned occurrences of lacking or reduced upper I 2, lower I 1, P 1 and M 3 there was found only one other tooth to be congenitally absent, i.e., a lower left canine in an adult *Cebus*.

Malformed single teeth, evidently caused by some disturbance in the early development of a tooth bud, are represented in the present material by the following four cases, besides the already mentioned incidences of supernumerary teeth, due to complete " twinning " of a tooth bud : Incomplete doubling of the crown of one upper central incisor in two adult *Alouatta* (Fig. 6, No. 10). Abnormal branch of the root of an impacted upper canine, reaching clear into the nasal cavity, in an adult *Ateles* (Fig. 6, No. 3). Finally, the most unusual condition is the multiple crown of a lower canine in an adult *Alouatta* (Fig. 6, No. 8).

Of crowded or misplaced, impacted and rotated teeth there is also a very considerable number, of which a few examples are shown in Fig. 6. All these cases exist in second dentitions among the incisors and premolars with only three exceptions, namely three adult *Ateles* in which the upper M 2 and M 3 of one side have become misplaced lingually. Crowded and rotated incisors have been noted only among *Alouatta* (four times in the upper and five times in the lower jaw), i.e., in the species distinguished also by its many lacking or vestigial incisors. This crowding is as often labial as lingual and rotations are for nearly to fully 90° ; both kinds of these abnormal positions produce a

reduction in the total width of the row of incisors. Misplaced and twisted premolars are often associated with retained deciduous molars, as in the *Alouatta* No. 5 in Fig. 6, but in other cases their misplacement may be directly caused by lack of space, as in the *Ateles* No. 4 in the same figure. The following are the cases with clearly abnormal positions of premolars, which hence do not occlude properly :

upper r. & l. P 1 crowded lingually, r. & l. P 2 labially in 1 *Ateles*
upper r. & l. P 1 crowded lingually in 2 *Alouatta*
upper r. & l. P 3 crowded lingually in 1 *Alouatta*
upper r. P. 1 crowded lingually in 1 *Alouatta* & 1 *Ateles*
upper r. P 2 crowded labially in 1 *Alouatta*
upper r. P 2 crowded lingually in 1 *Ateles*
upper r. P 3 crowded lingually in 1 *Alouatta*, 1 *Cebus* & 1 *Ateles*
upper l. P 3 crowded lingually in 1 *Ateles*
upper l. P 3 crowded labially in 2 *Ateles*
lower r. P 2 crowded labially in 1 *Ateles*
lower r. P 3 crowded lingually in 1 *Ateles*
upper r. P 2 deeply impacted in 1 old *Alouatta*
upper r. & l. P 3 rotated 180° in 1 *Alouatta*
upper l. P 3 rotated 90° in 1 *Ateles*

It will be noted that these irregularities of premolars are most frequent in *Ateles* and very rare in *Cebus* and that they occur far more often in the upper than in the lower jaw. The prevalently lingual crowding of indiscriminately first, middle or last upper premolars stands probably in some connection with the process of shedding the deciduous molars.

How extensively the dental apparatus can become diseased and destroyed in these wild platyrrhines is shown by the examples in Plate 3 and the first three sketches in Fig. 6. The frequency of carious cavities, alveolar abscesses and the loss of teeth *intra vitam* increases enormously with advance in age. Not a single instance of these pathological conditions could be discovered in any infantile or juvenile specimens of the present series. Only after adulthood has been reached do these conditions appear in rare cases of the age group *O*, but with rapidly increasing frequency in the following age groups, as is demonstrated by the data in Table 30. The frequency of caries differs strikingly among wild non-human primates, caries being very rare in *Alouatta* in contrast to most other platyrrhines, much rarer in all Colobinae than in Cercopithecinae, and not nearly as common in gorillas as in chimpanzees according to Colyer (1936) as well as the writer (1935 and 1956 b). In the present material it is again *Alouatta* which has only two cases of caries among 378 adults (=0·5 per cent), whereas the 118 adult *Cebus* contain ten skulls with caries (=8 per cent) and the 203 adult *Ateles* twenty (=10 per cent). On the other hand, alveolar abscesses differ little in regard to their prevalence in all three genera. There can be little doubt that all teeth, lost before death, had been preceded by abscesses, of which traces frequently can still be seen even though the alveolus has become closed and its walls have been largely resorbed. From Table 30

TABLE 30

Age changes in the percentage frequency of adult specimens with carious, abscessed and lost teeth.

Genus	Age Group	Total of Specimens	Percentage of Specimens with		
			Caries	Abscess	Closed Alveol.
Alouatta	0	123	0	4	2
	1	219	0.5	26	7
	2	36	3	75	17
Cebus	0	49	2	4	2
	1	61	8	18	7
	2	8	50	75	37
Ateles	0	72	1	6	0
	1	110	12	28	5
	2	21	29	67	29

it is very evident that wild platyrrhines quite frequently do outlive their misnamed " permanent " dentitions.

According to Fig. 7 caries is generally more frequent in the upper than in the lower jaw and affects by far most frequently the upper middle incisors. The latter teeth are also abscessed or lost more often than most other teeth. Abscesses are slightly more common in the upper than in the lower jaws of *Cebus* and of *Ateles*, but in *Alouatta* there is no such difference. The only significant sex difference in the relative frequencies of diseased teeth has been found for abscessed or lost canines. In *Alouatta* twenty-nine out of thirty-eight abscessed or lost canines are those of males, in *Cebus* the corresponding figures are nine out of thirteen and in *Ateles* twenty-one out of thirty-one. It seems that the long canines (or their deep sockets) of males are particularly prone to become broken or wrenched, thus leading to infections and abscesses more often than in females.

SUMMARY

For this study has been available a total of over nine hundred skulls of howler monkeys (*Alouatta palliata*, Gray), capuchin monkeys (*Cebus capucinus*, Linnaeus) and spider monkeys (*Ateles geoffroyi*, Kuhl) from localities ranging between the Panama Canal and Southern Mexico. In this vast and varied area the natural habitat for monkeys is far from continuous and uniform and there occur many factors favouring isolation. Furthermore, inbreeding is the rule among wild non-human primates (Carpenter, 1955) so that one could expect many different local races or even species among these platyrrhines

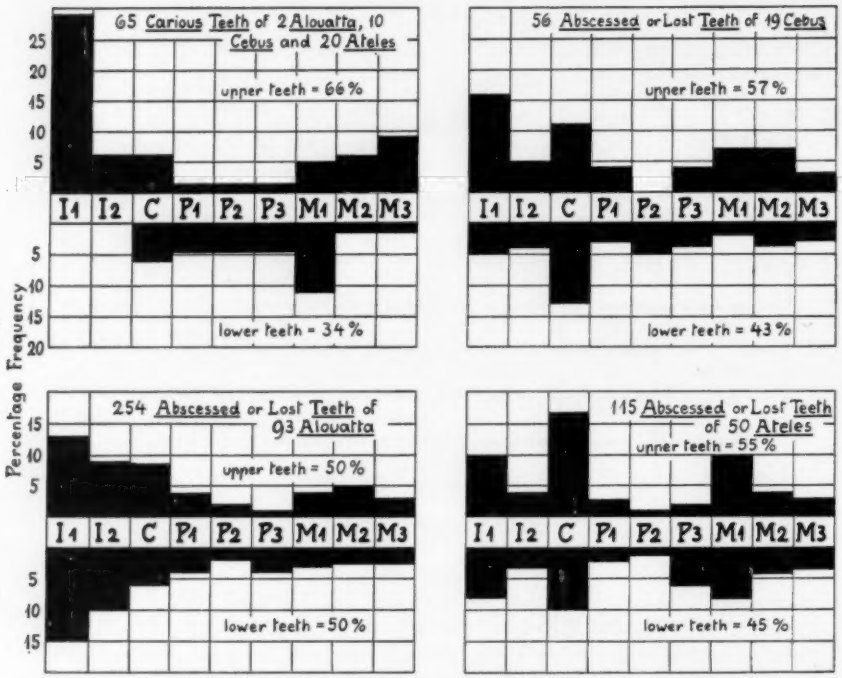
65 Carious Teeth of 2 Alouatta, 10 Cebus and 20 Ateles
upper teeth = 66%
lower teeth = 34%
56 Abscessed or Lost Teeth of 19 Cebus
upper teeth = 57%
lower teeth = 43%
254 Abscessed or Lost Teeth of 93 Alouatta
upper teeth = 50%
lower teeth = 50%
115 Abscessed or Lost Teeth of 50 Ateles
upper teeth = 55%
lower teeth = 45%
I1 I2 C P1 P2 P3 M1 M2 M3
Percentage Frequency

Fig. 7.—Percentage frequencies of caries, abscess and closure of alveolus among the different permanent teeth of adult *Alouatta*, *Cebus* and *Ateles*.

and, indeed, numerous ones have been described, though mostly on the basis of external features only. In regard to the characters of the skull and teeth, however, extremely little could be found in the present, large series which differs locally to a really significant extent. There always occurs such wide overlapping in the ranges of variations of local series that there hardly seems to be any justification for reliable and clear racial distinctions, recognizable in the skull. Even in regard to general size it can merely be claimed that in some isolated localities a majority of the individuals *tend* to be slightly smaller (or larger) than in some other localities.

The chief purposes of this paper are not so much taxonomic ones, as rather the finding of the exact degrees of intraspecific variability in cranial and dental characters and of the relative amounts of sexual differentiation and of postnatal age change for ultimate comparisons with the same conditions in other primates, including man. In addition this unusually large material lent itself for showing the frequency of malformations and diseases of the skull and teeth of monkeys in their natural habitat.

From 19 to 29 per cent of the specimens in the present material are immature (inf. + juv.) and from 5 to 8 per cent are " senile ". Among the

immature specimens there are more males than females in *Cebus* and *Ateles*, but in *Alouatta* the females form the great majority. Among adults the number of males for each 100 females has decreased in all three species, namely to 57 in *Alouatta*, 61 in *Ateles* and 103 in *Cebus*.

Secondary sex differentiation of the skull is very much greater in *Alouatta* than in *Cebus*, and in *Ateles* it is in general almost non-existent. The averages of the relative sex differences in fourteen cranial measurements equal roughly 10·0 in *Alouatta*, 5·5 in *Cebus* and only 0·7 in *Ateles*. Exactly corresponding values vary between 2·7 and 4·1 among *Colobus* monkeys and amount to 3·3 in chimpanzee and to 3·1 in man. In regard to cranial indices the sex differences are also most marked in *Alouatta* and least in *Ateles*.

The absolute size of cranial measurements varies on a general average somewhat less in *Cebus* than in the other two species and slightly less in females than in males. Cranial indices are also least variable in *Cebus*, but less variable in females only in *Alouatta*. The absolute as well as the relative measurements of the facepart of the skull are in all these species and in both sexes much more variable than those of the brainpart. The height and curvature of the forehead show an especially great variability among adult spider monkeys.

The number of infraorbital foramina on each side varies between 1 and 7 and that of mental foramina between 1 and 5, the average numbers differing according to species, but not to sex. The zygomatico-orbital foramina vary extensively in their size only in *Ateles*. A cranio-pharyngeal canal was found to persist in 16 per cent of *Ateles*, 0·8 per cent of *Alouatta*, but never in *Cebus*.

The postnatal age changes of the skull could be analyzed in considerable detail with the available material and they have also been compared with corresponding changes in series of skulls of chimpanzee and of man. In all of these primates the length of the braincase increases more than the breadth but the former grows less intensively than the length of the skullbase, hence the neuro-cranium becomes relatively narrower with advancing age and the cranio-vertebral joint shifts aborally. The latter change is most pronounced in *Alouatta* and greater in males than in females. The facepart grows postnatally much more than the brainpart and projects gradually farther forward in all these species. The average total increases of the measurements, expressed in percentage of the averages for infants, amount to 29 in *Cebus*, 36 in man, 45 in *Ateles*, 50 in *Alouatta*, and 55 in chimpanzee. Only in *Alouatta* is this ontogenetic change clearly greater in males than in females.

With the separation of all adult skulls into those having practically unworn teeth, those with medium dental wear and the remaining ones with extreme erosion and other indications of senility it became possible to analyze some of the age changes which continue after adulthood had been attained. Most of the many cranial measurements taken have significantly higher averages in the second age groups than in the first ones, so that the conclusion seems justified that the skull continues to grow at least in some parts from early to middle adult life. In the oldest series a majority of the measurements average slightly less than in the middle-aged series, indicating some senile atrophy. The distance between the right and left temporal lines decreases in its averages during the entire adult life span and this most markedly in males.

The metopic suture begins to close early in infantile life, but can remain partly open until the beginning of the juvenile period, when the occipital elements start to become fused. The mandibular halves are not fully united until all deciduous teeth have erupted in *Cebus* and slightly later in *Alouatta* and *Ateles*. The main sutures of the neurocranium all tend to close much earlier during adult life in *Alouatta* than in the other two species. In *Ateles* the coronal, sagittal and lambdoid sutures are still open even in many old specimens. In *Alouatta* it is the internasal suture which stays open much longer than in the other species and *Cebus* is distinguished by the early obliteration of its inter-maxillary sutures. A surprisingly high number of cases with abnormal suture closure has been encountered. For instance, the coronal suture of one side only has closed prematurely and thereby produced marked asymmetry in three *Ateles* and nine *Alouatta*. Single or multiple bregmatic fontanellar bones exist in 42 per cent of *Ateles*, 16 per cent of *Cebus* and 0·2 per cent of *Alouatta*. Lambdoid fontanellar bones are much rarer, being present in 11 per cent of *Ateles*, 3 per cent of *Cebus* and never in *Alouatta*.

The sequence in the eruption of the teeth was found to be as follows : The first dentition appears in the order i1 — i2—m1 — m2 —(c m3) in *Alouatta*, but in *Cebus* the c erupt before, instead of after, the m2 according to the few relevant specimens. The eruption of the permanent teeth occurs normally in all three species in the order M1 — I1 I2 M2 — (P1 P2 P3) — C M3, the P appearing in rapid and rather variable succession and the lower teeth generally well before the corresponding upper ones.

Overbite of the incisors is extremely rare in *Alouatta*, but common in *Cebus* and *Ateles* among which its frequency undergoes some changes with age.

Of clearly pathological conditions in the skull the following are most noteworthy : more or less well repaired fractures exist in fifteen *Alouatta*, four *Cebus* and three *Ateles*, all but one adult and most of them males. These fractures had occurred almost exclusively on the mandible, the zygomatic arch and the supraorbital rim. Irregular bony perforations, following infections, had developed in the walls of the frontal sinus in five *Cebus* and in the walls of one maxillary sinus in one *Alouatta* and one *Ateles*, also invariably adult specimens. Arthritic changes in one or both temporo-mandibular joints, previously never found among platyrrhines, have now been discovered in one *Alouatta*, one *Ateles* and five *Cebus* all of which are fairly or even very old animals.

A surprisingly large number of developmental abnormalities of the permanent teeth exists among all three species. Supernumerary molars have been found in two *Ateles* and one *Alouatta* and extra premolars in two other *Alouatta*. Congenitally missing permanent incisors could be recorded for eighteen *Alouatta*, but only one *Ateles* and no *Cebus*. One of the first premolars is lacking in five cases and one or two third molars in two *Alouatta*, three *Cebus* and nine *Ateles*. The last molars, particularly the upper ones, are furthermore frequently reduced in size and number of cusps and roots among all three species. Disturbances in the development of teeth have resulted in a number of unusual malformations of crowns or roots and have produced

many cases of crowded, rotated and impacted teeth. Especially frequent are lingually misplaced upper premolars of *Ateles* and of *Alouatta*.

Carious cavities and alveolar abscesses have not been encountered in a single infantile or juvenile specimen of the present series, but among adults these pathological conditions appear with increasing frequency to become mostly very common in the oldest age groups. Whereas caries is extremely rare in *Alouatta*, it exists in 8 per cent of adult *Cebus* and in 10 per cent of adult *Ateles*, affecting especially the upper middle incisors. The percentage frequencies of specimens with at least one alveolar abscess rise from only four to six among the youngest adults to 67 to 75 among the oldest. Alveolar closure, following the loss of teeth, also was found in at most only 2 per cent of the youngest adults, but in 17 to 37 per cent of the oldest ones, among which many have evidently outlived their " permanent " dentitions, due to erosion and disease. Abscessed or lost canines are particularly common in males, but there is no marked sex difference in the incidence of pathological changes in any of the other teeth. The prevalence of abnormal conditions of one sort or another in the permanent dentitions of these wild American monkeys is much greater than that which has been found by the writer (1942, 1958) among wild proboscis monkeys and guerezas.

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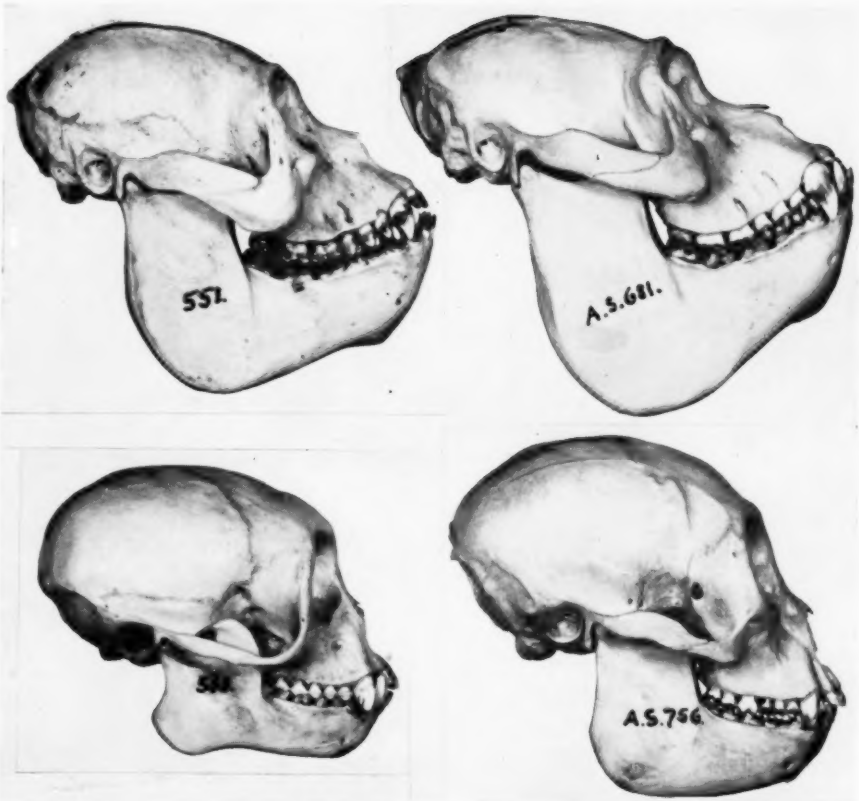
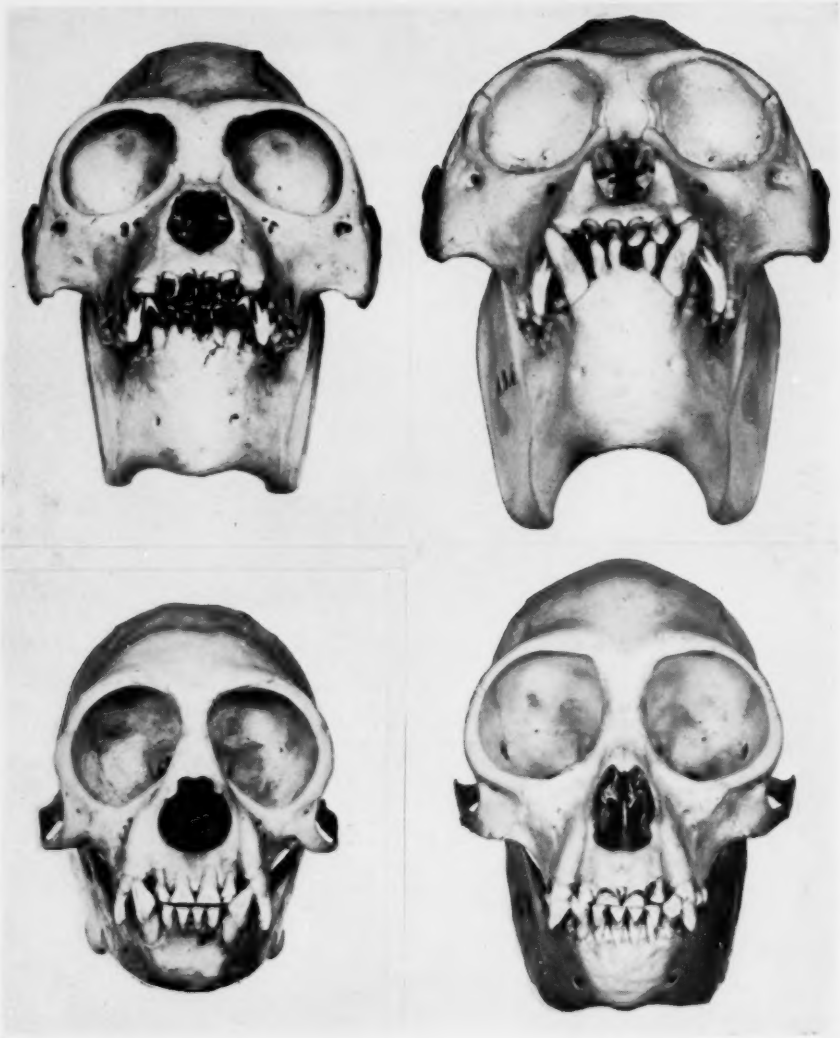
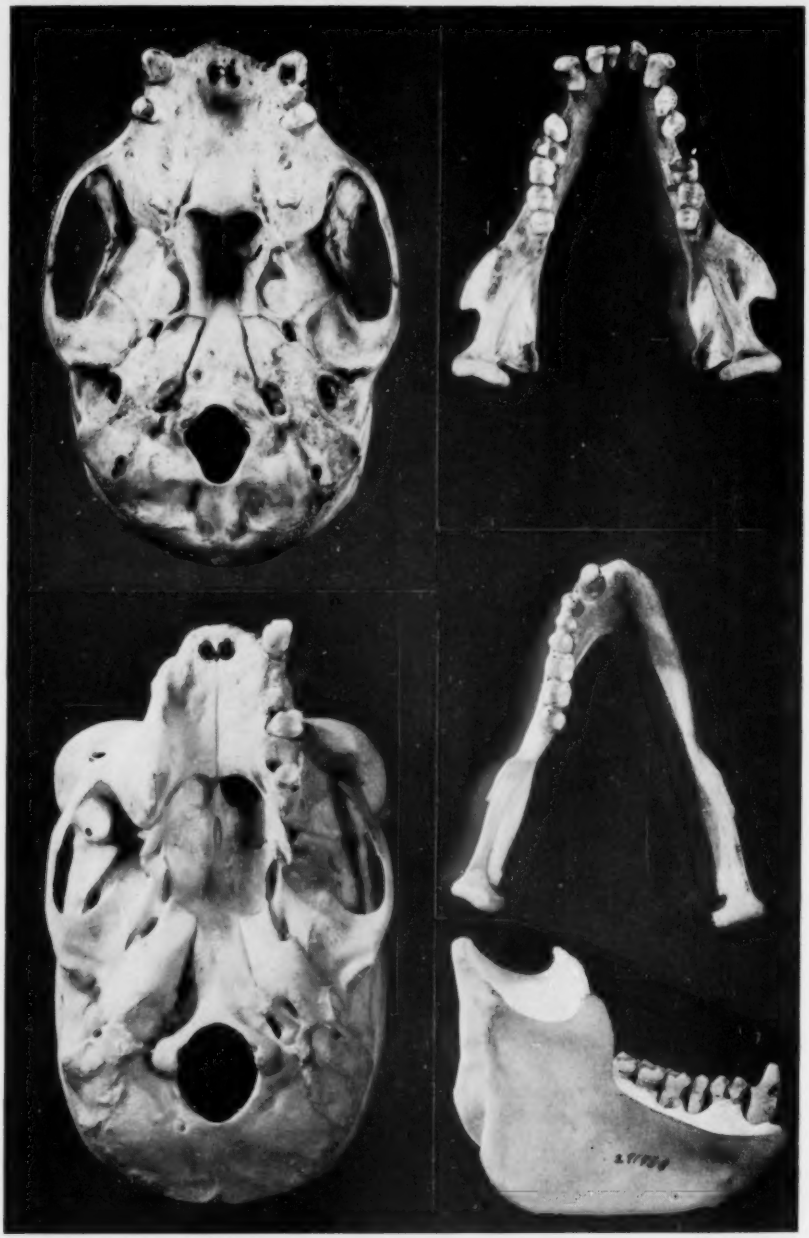


Side views of typical skulls of adult Nicaraguan *Alouatta* ♀ (top left), *Alouatta* ♂ (top right), *Cebus* ♀ (bottom left) and *Ateles* ♀ (bottom right). All reduced the same amount and posed in the ear-eye horizon.



Front views of the same four skulls as shown in Plate I.



Extensive destruction of the dental apparatus in an adult ♀ *Cebus* (top) and an adult ♀ *Ateles* (bottom, with 2 views of mandible). Both these Panamanian specimens are from the collection of the U.S. Nat. Mus. (Nos. 179041 and 291968). Note carious cavity in lower left C of the *Ateles*.

A NOTE ON THE EVOLUTION OF STRIDULATION WITHIN THE FAMILY SCORPIONIDAE

BY

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[Accepted 9th December 1958]

(With 1 plate and 2 figures in the text)

CONTENTS

	Page
Introduction	391
Behavioural origin of stridulation in *Heterometrus* and *Pandinus*	392
Correlation of different behaviour patterns with different stridulatory apparatus	393
Possible functions of precursors of stridulatory bristles	395
Possible origin of stridulatory mechanism in *Opisthophthalmus* ..	397
Summary	398
Acknowledgments	398
References	398
Explanation of the plate	399

INTRODUCTION

Pocock (1896 a) recognised the difference between the stridulatory apparatus of the two scorpion genera, *Heterometrus* (=*Palamnaeus* sensu Pocock) and *Pandinus* (=*Scorpio* sensu Pocock) as being of generic value. In *Heterometrus* (Fig. 1c) the sounds are made by the movement of a " keyboard " of basally flattened bristles on the pedipalp coxa (*H. str. br.*) against a " rasp " of finely striated cuticle on the coxa of the walking leg (*H. str. p.*), while in *Pandinus* (Fig. 1a) the position of the " keyboard " (*P. str. br.*) and the " rasp " (*P. st. p.*) is reversed, the former on the coxa of the leg and the latter on the pedipalp. In a recent paper on the subject of stridulation in scorpions (Alexander, 1958) it was suggested that the stridulatory movements in both genera might have arisen as an elaboration of a threat display involving the pedipalps, namely that of " intention-clutching " at the threatened object. It was admitted that the mechanisms, though superficially so similar, must nevertheless have evolved independantly. How this had come about however remained obscure. Since then I have had an opportunity to watch the stridulatory movements of *Pandinus* and it has become clear that the attempt to derive the stridulation of both genera from intention clutching was an oversimplification, and it is now possible to suggest an explanation for the evolution of the two distinct mechanisms.

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BEHAVIOURAL ORIGIN OF STRIDULATION IN *HETEROMETRUS* AND *PANDINUS*

From Figs. 1 a and c it can be seen that the stridulatory bristles of *Heterometrus*, which occur on the pedipalp, occupy a more lateral position than do those of *Pandinus*, situated on the first leg. In each case the rasp occupies a corresponding position on the other appendage. This difference can be described by referring to the stridulatory apparatus which occurs in *Pandinus* as the " mesial mechanism ", in contrast to the " lateral mechanism " of *Heterometrus*. It seems reasonable to assume that the specialised stridulatory bristles of the keyboards have been evolved as an elaboration of normal bristles and it is therefore desirable to examine the distribution of the coxal bristles in a scorpionid genus in which they are not specialised for stridulation. This is the case in *Opisthophthalmus*, of which *O. latimanus* Koch may be taken as an example. Fig. 1b shows the positions of the coxal bristles on the relevant appendages. Those on the pedipalp lie laterally, while those on the first leg are in the mesial position. Thus in *O. latimanus* there are unspecialised bristles in the two areas corresponding to those which the keyboards occupy in the mesial and the lateral stridulatory mechanisms. *O. latimanus* may therefore be said to show the preadaptations from which either type of stridulatory mechanism could have evolved.

In no species of *Opisthophthalmus* that I have examined is there any sign of structures which might be regarded as fore-runners of the rasps found in *Pandinus* or *Heterometrus*. The development of the rasp would therefore appear to be secondary, and the position at which it develops determined by the position of the evolving keyboard. Presumably there would be no selective advantage in the evolution of rasps until the elaboration of the bristles had reached a stage where their sound-production would be enhanced by the presence of a rasp.

Thus, if the assumption that the keyboards have been derived from unspecialised bristles is correct, the distribution of the latter implies that a mesial mechanism must have its keyboard on the first leg, while in the lateral mechanism they will inevitably be on the pedipalp. The next stage in our enquiry is therefore to discover how it has come about that *Pandinus* has evolved the mesial and *Heterometrus* the lateral type of stridulatory mechanism. As mentioned above, it was originally suggested that both might have arisen by the elaboration of the intention clutching movement. This idea was based upon the assumption made by Pocock (1896 b) that the stridulatory movements of *Pandinus* were similar to those of *Heterometrus* which Wood-Mason had described as " beating the air with its great pincers " during stridulation. The discovery that *Pandinus* does not stridulate in this manner does not contradict the actual observations made by Pocock, but his inferences from the anatomy were incorrect. I have recently been able to make some observations upon *P. imperator* Poc. in the Insect House of the Zoological Society of London. These make it clear that the movements of the pedipalps is not one characteristic of attack but of defence. The claws are not thrust out from the body as if to catch at the offending object but are drawn in towards the front of the scorpion and held across the mouthparts. In many cases the claws

themselves are in fact closed. Both pedipalpar attack and defence can be elicited in various species within the genus *Opisthophthalmus* without any accompanying pedipalpar stridulation and in some species such as *O. nitidiceps* Poc. either of the two threat movements may be evoked: which of the two appears seems to depend on how aggressive the scorpion is at that particular time. Plate 1a and b give some idea of the different appearance of the two behaviour patterns.

The conditions in which *P. imperator* will stridulate are similar to those described for *O. latimanus* (Alexander, 1958), so that here also the significance of the sound production appears to be that of threat. If we assume that the actual movement used in *Heterometrus* is correctly interpreted as being one of pedipalpar attack*, then the following tentative summary of the situation emerges.

Amongst the Scorpionidae the trend has been to develop powerful pedipalpar claws which are used for both attack and defence. In a situation in which threat display is appropriate, namely one where the animal shows tendencies towards both attack and flight, a number of autochthonous pedipalpar movements might occur and any one of these might conceivably be ritualised and accentuated by the addition of a sound component, resulting in a threat stridulation. In the case of *Heterometrus* the movement which was ritualised was that of clutching at whatever was being threatened by the scorpion : in *Pandinus* the movement was defensive, pulling the claws of the pedipalps in to cover the front of the animal.

CORRELATION OF DIFFERENT BEHAVIOUR PATTERNS WITH DIFFERENT STRIDULATORY APPARATUS

The next point which must be considered is the way in which the coxae of the pedipalp and first leg make contact with each other during the performance of the aggressive and the defensive movements. The first question is : do the points at which contact is made and friction occurs between the coxae differ in the two cases ? If they do, then we must see whether the difference may not explain why it is that the stridulatory mechanism evolved in *Pandinus* is the mesial one and that in *Heterometrus* the lateral. Duplicating the appropriate movements by manipulating the appendages of a freshly killed *O. latimanus* shows that the answer to the first question is that a clear difference does exist. Thus, in the pedipalpar attack, the coxae of the pedipalps are moved laterally from the neutral position (Fig. 2b) to that represented in Fig. 2c : this is to be expected as the whole pedipalp is held widely outspread in the final stage of the movement. In addition the coxae are rotated very slightly, so that their mesial surfaces tend to move dorsally, thus allowing the claws of the pedipalp to operate more nearly in the vertical plane, (see Plate 1a). The combination of these two movements results in the point on the pedipalp labelled *H. str. br.* in Fig. 1c and indicated in Fig. 2c by the broad arrow, moving laterally and ventrally and so coming into contact with the lateral part of coxa of the first leg beneath it. The clutching movement therefore induces friction

*Since this paper was submitted for publication the *Heterometrus* type of stridulation has been watched in an unidentified species of this genus and the interpretation suggested above is undoubtedly correct in this case.

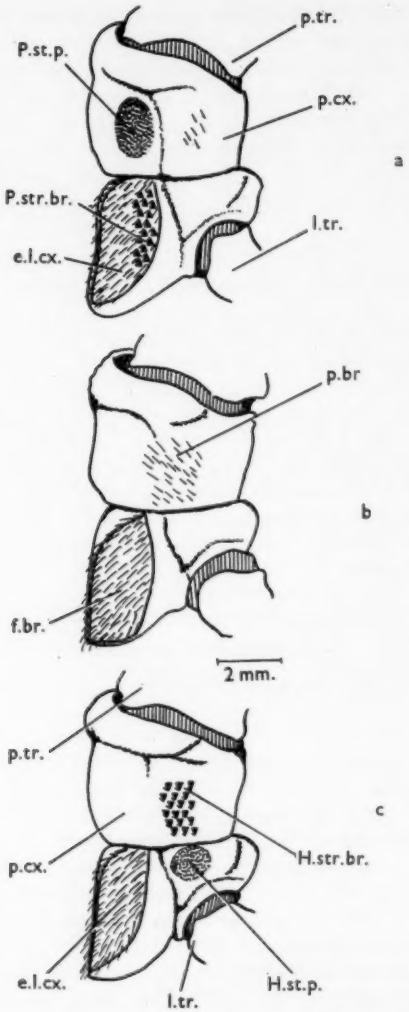

Fig. 1.—Diagrammatic representation of the coxae of the pedipalp and first walking leg of the right side of various scorpionids to show the position of the unspecialised and stridulatory bristles. The faces which normally make contact during the movement of the pedipalp have been separated, the pedipalp coxa, *p. cx.*, with its trochanter, *p. tr.*, is drawn above while below is the base of the coxa of the first leg *l. cx.* with its endite, *e. l. cx.* and, arising laterally and ventrally, the second joint of the leg, the trochanter, *l. tr.* The stridulatory bristles forming the "keyboard" are shown as black triangles while the striations of the "rasp" are mottled. Arthrodial membranes are cross-hatched. (a) The condition in *Pandinus imperator*; *P. str. br.*—stridulatory bristles on the coxal endite and thus in the "mesial position"; *P. st. p.*—striations. (b) The condition in *Opisthophthalmus* as

between the two surfaces which in *Heterometrus* constitute the lateral stridulatory mechanism. Selection for elaboration of this aggressive threat movement into a stridulatory display would be expected therefore to act on the " lateral preadaptation " seen in *O. latimanus*, not the mesial one. Thus the condition in *Heterometrus* is what would be expected if the theory that stridulation in this genus arose from a pedipalpar attack movement were correct.

The defensive movements, on the other hand, involve the whole of the pedipalp being drawn in towards the midline ; thus, when the pedipalps of the freshly killed *O. latimanus* are pushed into the appropriate posture, the coxae of the two sides are pulled together (Fig. 2a). Furthermore the femur-tibia joint is lifted so that the claws point down across the mouthparts (Plate 1b) and, as a result, the lateral parts of the pedipalp coxa must be swung dorsally. Consequently the coxal endites, which lie mesially, are depressed (Fig. 2a). Together these two movements tend to cause contact between the pedipalp coxa and the point labelled *P. str. br.* in Fig. 1a and indicated in Fig. 2a by the broad arrow. Thus there is friction between the two surfaces constituting the mesial stridulatory apparatus. Selection for elaboration of the defence movement would therefore be expected to result in the evolution of a stridulatory apparatus of the type found in *Pandinus*.

The argument may be briefly summarised as follows. It is suggested that the factor which was decisive in determining which type of stridulatory apparatus evolved was a difference in the behaviour of the two genera. In a " threat situation " the response of *Heterometrus* was mainly aggressive and intention clutching movements predominated, whereas in *Pandinus* the principal movements were defensive. The differences in the movements made in the two cases then conferred selective advantage on elaboration of devices increasing the noise produced by friction in lateral and mesial positions respectively. The first stage in this was elaboration of the unspecialised bristles already present in the two areas, i.e. on the first leg when friction was mesial (*Pandinus*—defensive) and on the pedipalp where it was lateral (*Heterometrus*—aggressive). The final stage in the elaboration of the stridulatory apparatus would then be the evolution of a rasp in the area rubbed by the keyboard bristles, i.e. on the pedipalp in *Pandinus* and on the first leg of *Heterometrus*.

POSSIBLE FUNCTIONS OF PRECURSORS OF STRIDULATORY BRISTLES

In both these genera the stridulatory bristles represent specialisations of already existing structures and to that extent the genera were " preadapted " for their respective modes of stridulation. The question may then be asked as to what was the original function of these bristles. To consider *Pandinus* first : in unspecialised forms these occur on the coxal endites of the first walking leg bristles which, together with others on the second leg, contribute

exemplified by *O. latimanus*. *f. br.*—feeding bristles on the coxal endite of the first leg in the " mesial position " and *p. br.*—prioprioceptive (?) bristles in the " lateral position ". (c) The condition in *Heterometrus*, drawn from a specimen of *Scorpio maurus* L. and modified to illustrate Pocock's account of the condition in *H. swammerdami*. *H. str. br.*—stridulatory bristles in the " lateral position " ; *H. st. p.*—striations.

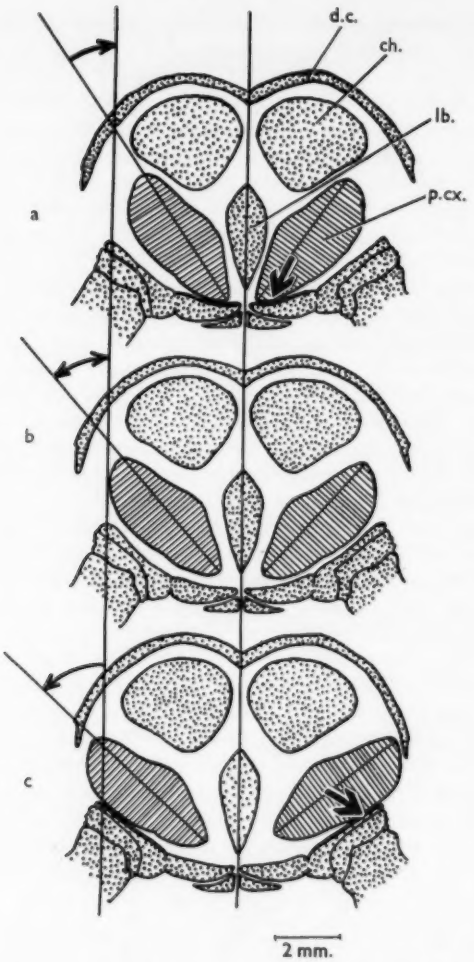

Fig. 2.—Diagrammatic representation of sections through the prosoma of *O. latimanus* to show the points at which friction occurs during various movements of the pedipalps. The dorsal carapace, *d. c.*, the chelicerae, *ch*, the labrum, *lb.*, the coxae, endites and trochanters of the first legs and the endites of the second are stippled, while the coxae of the pedipalps, *p. cx*, themselves are cross-hatched. The vertical lines serve to emphasise the lateral and mesial movement of the pedipalp coxae while the line through each of the coxae together with its angle from the vertical, indicates the rotation of this joint. (a) The relations during defensive threat, (b) The neutral position, and (c) the relations during attacking threat. It will be seen that in position (a) the mesial movement and rotation of the pedipalp results in mesial contact between the coxa of the pedipalp and first leg, while in (c) the opposite movements result in contact laterally. In both cases the point of contact is emphasised by a heavy black arrow : in (a) this point is homologous with that marked *P. str. br.* of Fig. 1a, while that of (c) is equivalent to *H. str. br.* of Fig. 1c.

to the formation of the feeding apparatus of the pre-oral cavity.* It is a part of this patch of feeding bristles which has been modified to form the "keyboard" of *Pandinus*. The function of the forerunners of the stridulatory bristles in *Heterometrus* is unknown. They may perhaps be proprioceptors in the same manner as the hair plates upon the legs of a cockroach (Pringle, 1938) : certainly they are innervated in *Opisthophthalmus*, but there is no positive evidence for this idea at the moment.

POSSIBLE ORIGIN OF STRIDULATORY MECHANISM IN *OPISTOPHTHALMUS*

Turning lastly to the stridulatory mechanism of the scorpions within the genus *Opisthophthalmus* itself, we find that neither the anatomical nor behavioural "preadaptations" which exist for the evolution of a pedipalpar threat stridulation have been utilised. In all cases where an animal of this genus is known to produce sound, it is the cheliceral stridulation, described for *O. latimanus* (Alexander, 1958) which occurs. Here the keyboard consists of basally flattened bristles carried upon the first joint of the chelicerae while the rasp is a finely granulated area upon a median keel formed from the inner surface of the carapace which projects downwards between the two chelicerae. As in the case of the pedipalpar stridulation of *Pandinus* and *Heterometrus*, both anatomical and behavioural preadaptations for the evolution of cheliceral stridulation can be recognised within the genus. In some species, such as *O. nitidiceps*, noise production is so slight that it is very difficult to believe that it can have any biological significance. In such cases the cheliceral bristles are present but they are unspecialised and lie only on the actual arthrodial membrane between the basal and second segment, not spread onto the sclerotised cuticle of the first segment as they do in *O. latimanus* and other stridulating species. The granulated rasp is also lacking on the under surface of the carapace and this is not developed into a ventrally projecting keel. Nevertheless it is clear that there is the anatomical basis for the development of the cheliceral stridulation which has been evolved in other species of this genus.

Those cheliceral bristles which may be elaborated to form stridulatory bristles have been found so far only within the genus *Opisthophthalmus*. Their normal function is unknown though it may possibly be similar to that suggested above for the pedipalpar bristles, that is proprioceptive.

It is clear from these results how the stridulatory mechanisms of these different scorpionids may have arisen, but as yet there is no information

* Snodgrass (1952) states that there is no feeding sieve in the preoral cavity of the scorpion, and that the small size of the mouth alone serves to prevent actual fragments of the prey passing into the pharynx. Snodgrass obtained his anatomical data from a species of *Centruroides* but it is clear that Buthidae and Scorpionidae differ slightly in this respect : buthids, though they do have bristles on the coxal endites, are conspicuously less hairy in this region than are the scorpionids. This difference in feeding apparatus may be simply correlated with a difference in feeding behaviour : the buthids macerate their prey far less than do the scorpionids, relying far more, presumably, on extra-oral digestion. Thus *Parabuthus*, *Tityus* or *Uroplectes* may leave pieces of disentergrated cricket as remnants of their meals while the scorpionids, *Opisthophthalmus*, *Opisthacanthus* or *Hadogenes*, leave small, hard pellets of thoroughly chewed chitin as remnants of similar meals.

which tells why *Opisthophthalmus* has evolved cheliceral rather than pedipalpar stridulation in spite of the fact that both anatomical as well as behavioural preadaptations for the latter were present. It seems possible however that a thorough study of the function of the unspecialised cheliceral bristles in this genus will suggest why they occur only in *Opisthophthalmus* and this, in its turn, may allow us to understand the selective pressures that led to this type of stridulation rather than any other.

SUMMARY

1. Superficially similar mechanisms of pedipalpar stridulation occur in the genera *Pandinus* and *Heterometrus*. The basic differences are pointed out and it is shown that part, at least, of the anatomical bases for both mechanisms occur in another scorpionid genus, *Opisthophthalmus*.

2. Contrary to previous opinions on the subject, it was found that the stridulatory movements in *Pandinus* and *Heterometrus* are not the same ; in *Pandinus* they are defensive while those described for *Heterometrus* correspond to the movement of pedipalpar attack.

3. It is pointed out that these two different movements produce friction in different places : the attack movement causes most friction over surfaces which produce the sound in *Heterometrus*, the defensive movement at the points which have become stridulatory surfaces in *Pandinus*.

4. It is shown that there is anatomical preadaptation to cheliceral stridulation within the genus *Opisthophthalmus*.

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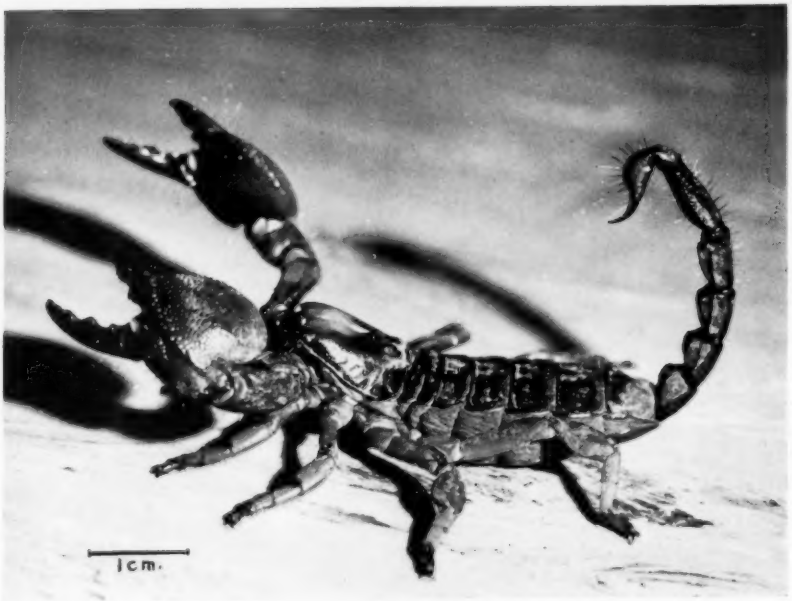

a

b

Opisthophthalmus nitidiceps. Female, showing threat display of the pedipalps.

EXPLANATION OF PLATE

PLATE 1

O. nitidiceps female showing threat display of the pedipalps.

(a) The attacking threat, pedipalps thrust forward away from the prosoma and the claws held so that they open and close almost in the vertical plane. (b) The defensive threat, pedipalps held down across the front of the prosoma and twisted so that their action is more nearly in the horizontal plane than it is in the attacking threat.

DEVELOPMENT AND STRUCTURE OF SOME ACTINOPTERYGIAN AND URODELE TEETH

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(With 2 plates and 2 figures in the text)

CONTENTS

	Page
Introduction	401
Materials and methods	402
Observations	402
1. The teeth of actinopterygians	402
(a) General considerations	402
(b) Establishment of the dental unit	404
(c) Formation and calcification of the enamel	405
(d) Formation of the dentine	408
(e) Attachment and eruption	410
2. The teeth of urodeles	411
(a) General considerations	411
(b) Teeth of the adult salamander	412
(c) Teeth of the hellbender	415
(d) Larval teeth	416
Discussion	419
Summary	420
Acknowledgments	421
Additional note	421
References	421
Explanation of the plates	421

INTRODUCTION

An understanding of the teeth of lower vertebrates has been much advanced by Kvam (1946, 1950). Particularly he has introduced the concept of " mesodermal enamel ", a hard outer covering which appears before the dentine in the development of lower types and hence initially in contact with the mesodermal pulp cells, in contrast to the " ectodermal enamel " of reptiles and mammals, which appears after dentine formation has begun and hence in contact with ectoderm only. The expression " mesodermal enamel " is adopted here for convenience, but it must be remembered that the odontoblasts themselves have an ectodermal origin in the amphibians at least (de Beer, 1947). The relationship between the two however is not at all clear ; is ectodermal enamel a peculiarity of the crossopterygian-tetrapod line of evolution, and hence present in crossopterygians, or is it a later development which appears only in tetrapods ? In this connection their precise distribution is important and here too some doubt exists. Kvam claims that mesodermal enamel

occurs in elasmobranchs, teleosts and amphibians ; for the first this appears correct (Kerr, 1955) and for the second verification is desirable, but among amphibians Gillette (1955) has shown that in the anuran bullfrog at least the enamel is certainly ectodermal. The groups therefore in which additional information on this and other aspects of the teeth appears necessary are the actinopterygians and urodeles, and their characteristic features have been described together to provide sufficient basis for a comparative assessment. For a bibliography of earlier work on urodeles see Gillette (above) and on teleosts see Levi (1939), Kvam (above) and Bertin (1958).

MATERIALS AND METHODS

Fish from a number of teleost families were examined, to find those most suitable for particular aspects of tooth structure and to serve as a comparative check. Those referred to in the text can be fully listed now and later designated by the English name only : trout (*Salmo trutta* L.), pike (*Esox lucius* L.), eel *Anguilla anguilla* (L.)), conger (*Conger conger* (L.)), hake (*Merluccius merluccius* (L.)), cod (*Gadus callarius* L.), haddock (*Gadus aeglifinus* L.), whiting (*Gadus merlangus* L.), saithe (*Gadus virens* L.), ballan wrasse (*Labrus ascanius* L.), gold sinny (*Ctenolabrus rupestris* (L.)), viviparous blenny (*Zoarces viviparus* (L.)), cat fish (*Anarhichas lupus* L.), grey gurnard (*Trigla gurnardus* L.), plaice (*Pleuronectes platessa* L.), angler (*Lophius picatorius* L.). Also available were *Polypterus senegalus* Cuv., *Calamoichthys calabaricus* Smith, *Lepisosteus osseus* (L.) and *Amia calva* L. The urodeles used were the spotted salamander (*Salamandra maculosa* Laur.) and the axolotl (larval *Ambystoma tigrinum* Green), with formalin-preserved hellbender (*Cryptobranchus alleghaniensis* Daub.) from Turtox and locally collected smooth newt (*Molge vulgaris* L.).

Routine fixation was by Bouin for general purposes, 95 per cent alcohol for calcification stages and 10 per cent formalin for argyrophil fibres ; decalcification was by 5 per cent nitric acid in 80 per cent alcohol, washed out with 80 per cent alcohol. Vacuum embedding was used and serial sections cut at 8 μ. A trichrome method (Weigert's iron haematoxylin-crystal ponceau-phosphomolybdic acid-fast green) was employed for general staining, Schmorl's methods for dentinal tubules and Dahl's alizarine for calcification ; Gomori's reticulum stain and PAS were also used. For whole mounts alizarine and glycerine gave clearest results, with dilute Parozone for maceration.

OBSERVATIONS

1. *The teeth of actinopterygians*

(a) *General considerations*

The nomenclature used in this account is illustrated in Fig. 1. The tooth itself has a transparent pointed tip, referred to simply as enamel, and below a column of dentine. Lining the interior face of the dentine is a layer of odontoblasts, with a central concentration of ordinary pulp cells. The outer face of the tooth is enclosed in the enamel organ, consisting of a single inner layer of cells in contact with the tooth—the internal dental epithelium or i.d.e.—and a single outer layer—the external dental epithelium or x.d.e. (James, 1953).

At the apex of this dental unit the x.d.e. is continuous with a cylindrical epithelial process, which forms a persistent connection with the basal layer of the epidermis or with the x.d.e. of an older tooth unit. Within the epithelial process there is a core of cells comparable with the outer cells of the epidermis, and between the i.d.e. and x.d.e. corresponding cells show an interesting variation in different groups of fish. In the primitive actinopterygians they form an open cellular tissue, most prominent in *Polypterus* (Pl. 1, fig. 1) but quite well developed in *Calamoichthys*, *Lepisosteus* and *Amia*, which recalls the stellate reticulum of reptiles and mammals; in lower teleosts (eel, conger) cells are still present in a restricted space between the two epithelia, but in more advanced forms (cod family) they are reduced in number or absent altogether. The epithelial process itself tends to be wide and straight in primitive fish, in later forms it is narrower and sometimes much convoluted (cod).

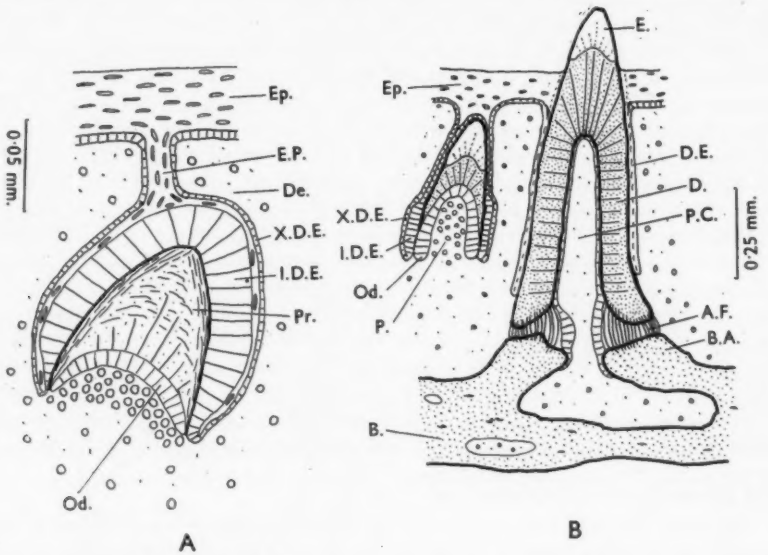

Fig. 1.—Formation of typical small jaw tooth of teleost (eel). A, diagram of pre-enamel stage. B, diagram of small replacement and mature tooth.

A.F., attachment fibres; B, bone of jaw; B.A., bone of attachment; D., dentine; De., dermis; D.E., i.d.e. plus x.d.e.; E., enamel; Ep., epidermis with basal layer; E.P., epithelial process with some enclosed cells; I.D.E., internal dental epithelium; Od., odontoblast layer; P., pulp cells; Pr., pre-enamel with fibres and processes in matrix; P.C., pulp cavity; X.D.E., external dental epithelium.

The relationship between new dental units and already established teeth varies largely according to functional requirements. When the functional teeth are scattered irregularly over an area, as occurs commonly on branchial pads but also in some jaws (eel, gurnard), the new units may be derived independently from any part of the basal ectoderm over the tooth-bearing area,

although even in these cases some can usually be found originating close to or from the sides of older units. When a greater degree of regularity is shown by the functional teeth, as alignment along the edges of the jaws (conger), the new units are usually derived from the inner x.d.e. faces of the old to give a one for one replacement. An extreme case of this condition is seen in the plaice, where each row of jaw teeth functions as a complete unit so that all must be replaced more or less together ; here the older teeth are shed during the winter and the new teeth, formed in units derived from the deeper faces of the old, move up in unison to occupy their places by spring. On the other hand in the anterior jaw teeth of the ballan wrasse, where the replacement teeth develop below the functional and a direct relationship between the units might be expected, the new units are in fact attached by long slender processes to the basal epidermis.

Variation is shown similarly in the attachment of the teeth to the underlying bones. The commonest condition is for tooth growth to be followed by the formation of a cylindrical bone of attachment, connected by fibres to the tooth at one end and fused to the underlying bone at the other, so permitting sufficient tooth movement to reduce the danger of fracture. Sometimes, however, the fibrous junction becomes solidified and calcified into a definite ankylosis, and sometimes the top of the bone of attachment is shaped to allow the tooth to swing inwards on a simple hinge from its resting position. In *Polypterus* no distinct bone of attachment is formed, so it appears probable that this structure has been evolved within the actinopterygians. The shedding of teeth is initiated by large granular phagocytic cells of characteristic appearance which destroy the bone of attachment, the connecting fibres and a varying amount of the base of the tooth in that order (Pl. 1, fig. 2). When the tooth projects noticeably above the surface (plaice) a quite restricted degree of erosion will allow it to be shed, but when only the tip is exposed (eel) then most of the tooth must be removed before this occurs. In serial sections such shedding stages are uncommon, as also are really early stages of development, so that tooth growth and turnover are probably quite slow.

(b) *Establishment of the dental unit*

The first stage of development generally mentioned is a cylindrical downgrowth of epidermal cells into the dermis, but the details of formation of this downgrowth are worth describing in the particularly clear case of the gurnard jaw, where the teeth develop independently of each other. The earliest detectable stage is a small lenticular concentration of dermal cells in contact with a flat disc of cells of the basal layer of the epidermis, hypertrophied centrally and grading off into the ordinary cells of the layer peripherally (Pl. 1, fig. 3) ; both ectodermal and mesodermal components appear equally involved, so that it is not possible to say which is primarily responsible (but see de Beer, 1947). Increasing enlargement of the epidermal cells causes the disc to buckle inwards at its edges ; subsequent growth pushes it deeper into the dermis as a wide cylinder, bounded by a regular cubical epithelium continuous with the basal layer and filled with an irregular core of the more superficial epidermal cells. This cylinder narrows into a typical epithelial process as it grows in

length, but to what extent growth is due to migration of basal cells or to localised mitosis could not be determined. Finally the tip of the process is doubled inwards over the mesoderm concentration to form the cup-shaped enamel organ and the pulp (Pl. 1, fig. 4). At first both walls of the former have cells of the same cubical shape but as the tooth substance appears the i.d.e. cells become enlarged and very regularly columnar while the x.d.e. cells thin off, and at the same time the pulp cells adjacent to the tooth substance increase in size and granulation to form a distinct though rather irregular layer of cells which, until the dentine itself appears, can be called pre-odontoblasts. During these changes there occurs a loss of adhesion between the i.d.e. cells and the pulp over their area of contact, shown in sections by the tendency for a narrow space to appear between the two. This becomes clearly established by the cup stage but may well have begun with the first stage described. The actual line of separation is between the basal cells and the basement membrane, so that the latter remains with the mesoderm ; the persistence of this condition is seen later in the lack of attachment between the i.d.e. and the tooth surface.

A complicating feature of early development is a difference in orientation which develops between the epithelial process and the dental unit. Eventually the tooth is going to erupt by moving up the centre of the process and it might therefore be expected that the enamel organ cup and its young tooth would form at the inner end of the process and symmetrically to its long axis. In fact the cup develops to one side of the end (Pl. 1, figs. 4 & 5) ; not only so but it also develops to some degree across the end, so that the long axes of the two are not in the same plane and a section through the length of the process is not therefore a true longitudinal section of the tooth. The reorientation which takes place before eruption will be described later.

(c) *Formation and calcification of the enamel*

A first requisite is to determine the type of enamel present in these fish. For this purpose the jaw or branchial teeth of the eel, whiting and cod are very suitable in that they are numerous, medium sized and of typical teleost shape. In the mature tooth of each the enamel is a pointed cone, transparent unless pigment is present, which can be removed with acid to expose the top of the dentine, of an equally characteristic but quite different shape (Pl. 1, fig. 2). In development the tooth substances appears first between the i.d.e. and pulp in the deepest part of the cup ; it forms exclusively on the deeper side of the basement membrane and hence appears primarily at least to be a mesodermal production. The shape of the cup, and so of the very earliest tooth substance, is hemispherical, but at once a reshaping begins to produce a cone-shaped i.d.e. Within this cone the early tooth substance is built up into a structure of the size and shape of the adult enamel, and only when this is complete does the quite differently shaped apex of the dentine appear. The enamel of these teeth is therefore of mesodermal type, completely formed as an organic pre-enamel before dentine formation begins. The importance of the i.d.e. in determining the shape and orientation of the tooth is also evident (James & Wellings, 1943). The finer structure of the pre-enamel can now be described from a number of suitable species.

The pre-enamel contains fibres of different origins and sometimes cytoplasmic processes from the pre-odontoblast cells, all embedded in a more or less homogenous and lighter staining matrix. The isolation of individual pulp cells in the substance of the pre-enamel during its development, which occurs not uncommonly in elasmobranchs, has been seen in this material only very occasionally in *Polypterus*. The finer structure of the matrix itself is obscure but before calcification it is distinctly cohesive and may be microfibrillar, also its greenish trichrome staining reaction indicates a basically collagenous nature. The first type of fibres, and the most important in bulk in the bony fish, have no counterpart in elasmobranchs. They are laid down progressively and in such a manner that the pre-enamel is divided roughly into cortical and medullary zones (Fig. 1A). The fibres of the cortex are the first to appear and develop as long and fairly straight fibres laid down parallel to the outer surface of the tooth, they continue to form down the sides of the pre-enamel as development proceeds and later appear to continue uninterruptedly into the dentine. Those of the medulla, appearing somewhat later, gradate into the preceding but are arranged more or less parallel to the surface of the pulp, showing as curved and intermingling fibres with a higher proportion of matrix. Since the pre-enamel is built up from its inner end all these fibres are doubtless mesodermal in origin, but the pattern varies considerably ; for example, in the eel, whiting, haddock and others it is as described, in the gurnard the pre-enamel is almost homogeneous in appearance, and in the wrasses the medullary fibres are very distinct and much more complexly intermingled. All these pre-enamel fibres and indeed the connective tissue fibres in general, take silver too strongly for the reticular techniques to have much specific value, but one feature shown clearly is that occasional fibres from the pre-enamel pass through the pre-odontoblast layer to join the connective tissue framework of the pulp. The second type of pre-enamel fibres pass inwards from the basement membrane, more or less at right angles, to taper off and disappear within the substance of the pre-enamel before the dentine is reached. Their occurrence however is variable ; in the ballan wrasse and gold sinny they are very prominent both with trichrome and Gomori's reticulum stain, and may be the structures described by Mummery (1917) as enamel tubes ; in the cod and whiting they are finer though still distinct, but in the eel and the lower actinopterygians it has not been possible to demonstrate them at all. Their absence in these primitive fish makes their similarity to the reticular fibres of elasmobranch pre-enamel appear less significant.

The cytoplasmic processes from the pre-odontoblast cells, first described for teleosts by Kvam (1950) in the eel, are extremely slender and only clearly visible when in the plane of section. They have been seen most distinctly with trichrome in the eel, ballan wrasse, gold sinny and *Lepisosteus*, emerging from the rather square ends of the pre-odontoblasts as fine pink lines passing up lighter but otherwise ill-defined tubes into the green pre-enamel. Sometimes they are of considerable length, but do not reach the surface of the tooth. They appear to be quite comparable to the similar structures seen in elasmobranchs (Kerr, 1955). Their cytoplasmic reaction disappears as the pre-enamel begins to calcify and a similar pattern of radiating fibres take their place,

although owing to the delicate nature of the processes the actual derivation of the one from the other must remain to some degree presumptive. In the mature tooth this third type of fibres is represented by fine lines radiating through the transparent enamel from the top of the dentine. In teleosts they have too little coherence to withstand decalcification, but in *Lepisosteus* the careful application of acid leaves a fringe of these fibres surrounding the long central core of dentine. In the cod family it has not been possible to detect either the processes or the corresponding fibres ; in these fish also, unlike the foregoing, no dentinal tubules develop later in the dentine.

When the pre-enamel is fully formed the dentine begins to make its appearance, but just before this happens the pre-enamel commences to calcify. The pattern of deposition of the calcium salts has been followed in the plaice, since a line of early replacement teeth can here be conveniently dissected out still enclosed in a strip of tissue and sectioned without decalcification ; for reasons mentioned earlier these teeth are all in about the same stage of development, and for early calcification should be obtained during May and June. The tooth is quite broad with the enamel stretched across the whole of its cutting edge, so that the pre-enamel is of similar shape. The calcium salts, stained by Dahl's alizarine, show first as a transverse oval patch which appears in the medullary zone of the pre-enamel without any obvious relationship to the adjacent cell layers. The staining reaction of the original patch, cut across its central region in the illustration (Pl. 1, fig. 6), intensifies and spreads outwards as the dentine appears below, finally reaching the surface of the tooth. In the oldest stages which can be sectioned the calcified enamel is tending to fragment, and is becoming glassy and resistant to staining ; this change however does not commence at the original locus of deposition but instead spreads downwards from the cutting edge of the tooth. A comparable series of preparations can be made as whole mounts, both in the plaice and other fish, in which the area of deposition appears initially as whitely opaque and stains readily with alizarine or silver nitrate. In the cod and others a yellow pigmentation of the enamel accompanies calcification.

In sections of decalcified material from all the species examined related changes can be seen in the pre-enamel during the course of its calcification. In the pre-enamel of teleosts both fibres and matrix show first a loss of staining affinity and then of cohesion, the reaction appearing first in the medullary zone and spreading outwards in association with the deposition of the calcium salts, so that finally no trace of the organic framework of the pre-enamel is to be found in decalcified sections and only an enamel space remains. A series of stages in this process can be recognised : first to disappear is the substance of the medulla, so that the remains of the cortical fibres enclose a space occupied only by the radiating process fibres from the apex of the dentine (seen well also in *Polypterus* Pl. 1, fig. 1), next the latter go and the long cortical fibres disappear from the tip of the tooth downwards, so that the penultimate stage in reduction is a fringe of these cortical fibres attached around the edge of the dentine. In the more primitive fish the same sequence of changes occurs but some remains of the original framework may persist, particularly in *Lepisosteus*. The removal of the apparently collagenous pre-enamel by some process

which leaves the collagen framework of the adjacent dentine quite unaffected is not reflected in any pronounced histological difference between the two tissues before calcification ; during the course of its disintegration however the pre-enamel does show a much increased PAS affinity. The i.d.e. cells during calcification undergo a further enlargement, with vacuolisation and other signs of activity which vary markedly with the species, but no trace of calcium reaction has been found in these cells at any stage (cf. Levi, 1939). Of the fish examined these changes are least pronounced in *Polypterus* and reach their climax in the cod and hake. The elaborate vascularisation of the enamel organ, in the region of the enamel itself, which accompanies calcification in the wrasse teeth has been fully described by Kvam (1950). As calcification ends the i.d.e. cells collapse to a fraction of their maximum size and form a thin double sheet with the x.d.e. cells.

(d) *Formation of the dentine*

The open end of the enamel organ continues to grow deeper into the dermis, keeping always a little in advance of the developing tooth, and the first dentine appears as a ring round the edge of the pre-enamel cone. Rapidly however it extends across the whole inner surface of the latter to form the dentine apex of characteristic shape, a central mound with a peripheral rim (Fig. 1B), which varies only in proportions in different fish. The earliest dentine to be laid down forms a narrow band of what appears to be denser tissue, frequently with a slightly different staining reaction. Later formation of dentine consists of a growth in length inwards against the basement membrane, which is incorporated into its surface, and in thickness by addition to its internal face. With the appearance of the dentine an odontoblast layer becomes defined and develops *pari passu* with the i.d.e., so that between these two layers the forming dentine gradates off into the basement membrane which in turn passes round the edge of the enamel organ on to the outer face of the x.d.e. This thin inner end of the dentine cone may curve either outwards or inwards but becomes shaped into its final form as it thickens. The dentine itself consists of a framework of coarse fibres, felted together after their formation by a closely interwoven stroma of very fine fibres. Of the coarse elements some pass more or less radially from the basement membrane or the outer regions of the tooth and between the odontoblasts into the pulp, to be incorporated progressively as the dentine thickens ; this series, which shows up well with Gomori's reticulum stain, is quite numerous in early stages of development but later few or none can be seen, and the total contribution to the mass of the dentine is not great. The main series of coarse fibres, for which Gomori is also useful, are longitudinal and run the entire length of the tooth. In sections cut parallel to the surface of a tooth at the appropriate stage the earliest of this series often appear continuous with the thicker fibres of the pre-enamel cortex ; after the disappearance of the pre-enamel fibres their upper ends are embedded in the slightly modified dentine apex zone and their lower ends project freely from the inner end of the dentine cone into the dermis. Here they continue to lengthen and become progressively embodied into the tooth throughout development. A characteristic feature of teleost dentine is that groups of

these fibres are arranged in radially orientated longitudinal bands in a quite well defined zone in the outer part of the dentine, a feature most easily seen in transverse sections but occasionally visible in longitudinal sections cut in the plane of one of the bands (Pl. 1, Fig. 7).

As the enamel organ pushes deeper into the dermis to keep pace with dentine formation its i.d.e. cells show a reduced version of the changes which occurred in those cells covering the enamel ; at first they are cuboidal, during the main part of dentine formation at their level they become distinctly columnar and finally they regress to the flattened condition. Frequently all three stages can be seen at different levels in the same growing tooth, and in such cases the cells are closely applied to the tooth during the first two stages only. The degree of hypertrophy is less in primitive types, and always less than over the corresponding enamel. The lack of two separate stages in this hypertrophy in the case of the dentine is noticeable. After the completion of dentine formation the inner end of the enamel organ shrinks upwards somewhat and so no longer marks the inner end of the tooth, however the attachment of the basement membrane forms a convenient alternative landmark in determining the precise inner end of teeth which have no dentinal tubules and are fused to their bone of attachment.

As the dentine apex forms the pre-odontoblast cells, which appeared responsible for the pre-enamel, become converted into the odontoblast layer which in turn appears responsible for dentine formation. In most fish these cells are elongated rather than columnar, their nuclei staggered to allow closer packing, their cytoplasm granular and their outer ends truncated against the developing dentine ; the layer increases in extent with the elongation of the tooth but the cells retain their form throughout their period of activity, coinciding in the tooth itself with dentine formation, and then regress into attenuated cells similar to those of the dermis in general. The odontoblast processes into the dentinal tubules are always very slender, whether one or more originate abruptly from the truncated end of an odontoblast or whether the cell narrows into a single process, and the tubules appear to be built up round them as the dentine thickens and the cell bodies of the odontoblasts are displaced inwards. The processes into the apex of the dentine appear to be the persistent roots of the cytoplasmic processes which earlier penetrated the pre-enamel, but all are cut off by the developing dentine and no tubules have been seen to penetrate the dentine surface. The actual presence of processes in the tubules can readily be ascertained in early stages of development but in mature teeth they have not been detected at all, and the corresponding change in the form of the odontoblasts supports the possibility that the processes are then genuinely absent and the tubules filled merely with fluid (cf. James, 1957). In most fish the pattern of dentinal tubules is richest and most distinct round the top of the pulp cavity, laterally the tubules penetrate the band fibre zone but terminate well below the surface. In many fish however the tubules become progressively shorter down the sides of the tooth ; this feature shows well in *Amia*, where also the numerous bone-like lacunae and their cells which characterise these teeth are confined to the restricted basal zone penetrated by the tubules. A dentinal tubule system is present in all the primitive

actinopterygians but tends to be suppressed in some families of teleosts, a tendency however not correlated with the suppression of the bone lacunae ; for example both tubules and lacunae are present in the eel and conger, the tubules only in the plaice and angler, and both are absent in the gurnard and cod. In the cod also as in others of that family, an enclosure of pulp blood vessels during later dentine growth produces an inner zone of vascular dentine.

(e) *Attachment and eruption*

A great deal of detail variation occurs in different teleosts but the normal method of tooth attachment, by an annular ligament and a bone of attachment, is well shown by the eel, whiting and cod. Here the layer of odontoblasts does not terminate, as does the i.d.e., at the inner end of the tooth, but is continued inwards as cells of similar appearance and arrangement which are associated with the formation of the later structures. The annular ligament consists simply of extensions of the coarse longitudinal fibres of the dentine into the dermis beyond the end of the tooth proper and no longer bound together by the close meshwork of finer fibres ; even the bands of grouped fibres can at times be followed through the ligament (Pl. 1, fig. 7). After a short free course these fibres become felted together again and calcified into a bone-like tissue, which lacks dentinal tubules but possesses a few lacunae in fish where such normally occur ; this bony tissue forms free in the dermis and is at first ring shaped, with the " odontoblast " layer extending down the inner face of the ligament and curving round the bone of attachment so as to enclose it on three sides. The ring is built up into a short tube, with perforations in its walls for the passage of blood vessels and dermal tissue, and its inner end finally fuses with the main bone below; at the same time the "odontoblasts" again lose their characteristic appearance to become indistinguishable from ordinary dermal cells. Simple hinge joints are frequently formed by an appropriate shaping at the top of the bone of attachment and a minor rearrangement of the fibres, such occur in cod jaw teeth and much resemble the condition described later in urodeles.

The sequence of events leading to eruption can be most easily followed in teeth derived separately from the epidermis, such as occur in eel, cod and gurnard. At the end of pre-enamel formation the dental unit is attached at an angle to the inner end of the epithelial process, as previously mentioned, but during the early stages of dentine formation a reorientation is brought about. Exactly how this is achieved is not clear, but the effect is both to bring the tooth into its final axis of eruption and at the same time greatly to increase the number of central cells in the epithelial strand. When the strand is short (gurnard) the top of the unit may now come into direct contact with the epidermis, or where the strand is convoluted (cod) the convolutions may fuse into a single mass, but in all cases the final result is a wide column of epidermal cells up which the tooth points and will eventually erupt, without of course ever penetrating the basement membrane. On the other hand when the tooth unit is formed from the side of an older unit, by outgrowth from its x.d.e., then the epidermal column forms up the adjacent face of the older unit, so facilitating accurate replacement when the older tooth is shed. If now the

position of the tooth tip relative to the basal layer of the epidermis is noted then the beginning and extent of eruption can be accurately assessed, and both vary a good deal. In the simplest condition the dermis is sufficiently thick to allow the tooth to complete its growth in length without interference from the main bone below, and in such cases eruption appears to be conditioned primarily by growth of the bone of attachment. In the eel the latter is relatively small so that movement outwards of the tooth is not great and its tip protrudes little above the surface of the epidermis ; indeed in this fish the removal of the flattened i.d.e. cells over the tip appears to result from actual use of the tooth and may never occur at all (larger tooth in Pl. 1, fig. 2), whereas in the cod eruption is much more pronounced. More usually however the inner end of the tooth approaches the underlying bone before the tooth has reached its full length, due to a narrow dermis or a relatively long tooth, and movement outwards then commences before the bone of attachment appears and eruption is a combined growth effect of both. Among earlier forms *Polypterus* shows eruption due to tooth growth and the bone of attachment represented merely by a low circle of fusion tissue between the tooth and the bone of the jaw ; in this fish also occasional cells in lacunae appear in the last dentine to be formed, and there is considerable fusion between the bases of the teeth themselves.

2. *The teeth of urodeles*

(a) *General considerations*

In the species examined the adult teeth show a comparatively narrow range of variation upon a simple structural pattern, although the functional significance of the shape itself is not clear. A cone of dentine, often curved inwards and flattened somewhat in the line of the jaw, is surmounted by a small bicuspid cap of enamel. The cusps, present also on the underlying dentine, are really two roughly parallel crescentic ridges which thin off down either side of the tooth ; a lingual ridge passing over the apex and a labial which varies in position in different species from quite near the first (axolotl) to well down the outer side of the tooth (hellbender). The teeth are attached by a ring of fibres to the upper ends of open cylindrical pedicels, fused labially to a thin flange arising from the bone below (Pl. 2, fig. 1). The replacement teeth are formed in a continuous dental lamina internal to the functional teeth, and replacement is more usually irregular than alternating. In tooth shedding phagocytes again appear ; the pedicel is eroded first and then much of the inner end of the tooth, and the tops of these old teeth are often visible as a broken line to the labial side of the functional teeth, but the flange from the bone remains intact.

In larval urodeles, with the exception of the axolotl in which both types may appear, the teeth are straight elongated cones with single enamel points, recalling the typical telost form. Relationships in the jaws are comparable to adults, though in the axolotl the lamina is further separated from the attached teeth and replacement still more irregular. Also in the inner series of axolotl teeth the pedicels, which may be reduced merely to rings, are carried

on an open bony framework, itself attached to the bone below. The flanges for the jaw teeth may therefore originally have arisen independently, though now inseparable in adult forms from the bone proper.

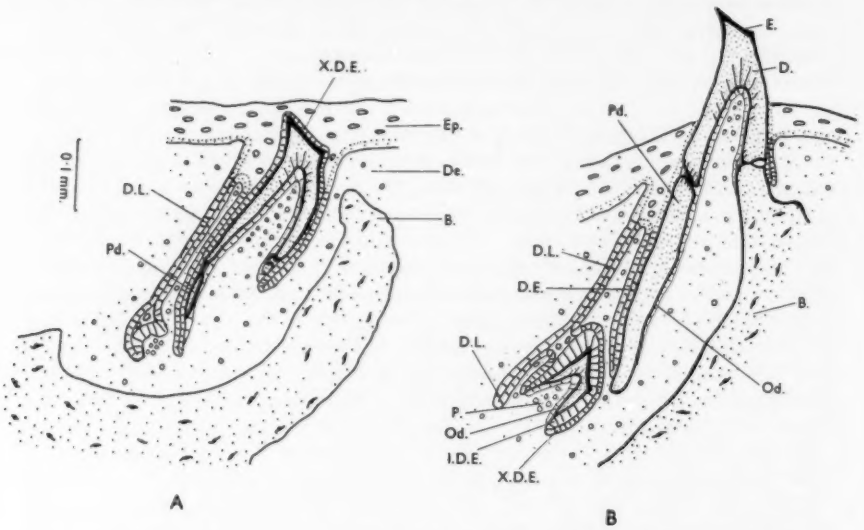

Fig. 2.—Formation of salamander bicuspid teeth. Edge of jaw to right. A, diagram of cup stage and half formed tooth unit. B, diagram of early stage and attached tooth. B., bone of jaw ; D., dentine ; De., dermis ; D.E., i.d.e. plus x.d.e.; D.L., dental lamina ; E., enamel ; Ep., epidermis with ill-defined basal layer ; I.D.E., internal dental epithelium ; Od., odontoblast layer ; P., pulp cells ; Pd., pedicel : X.D.E., external dental epithelium.

(b) *Teeth of the adult salamander*

The dental lamina extends round each jaw, as a doubling inwards of the basal cell layer of the epidermis to form a continuous sheet about 0·4 mm. deep just internal to the functional teeth ; its two walls are well defined, with some central cells between, and the dental units form on one face only. The first indication of a new unit is the appearance of a small concentration of mesoderm cells against a disc of enlarged laminar cells on the face of the lamina near its inner border. The disc deepens and enlarges into a shallow cup (Fig. 2A) whose axis is at first more or less at right angles to that of the lamina, but before any tooth substance has appeared the upper lip of the cup has grown outwards and downwards so that the axis becomes roughly parallel to that of the lamina, and this is the orientation in which the tooth itself will form. The cup develops into the enamel organ with a few isolated cells between its i.d.e. and x.d.e., comparable to the central cells of the lamina, but neither here nor in any other urodele examined do they show any tendency towards forming a stellate reticulum. As the tooth substance appears it incorporates the basement

membrane on to its surface, so that during subsequent stages the membrane can be seen attached to the tooth at the innermost border of the dentine, but since it cannot be differentiated upon the tooth surface its relationship to the enamel which develops later cannot be determined. Before the appearance of tooth substance also the network of reticular fibres in the dermis has numerous connections with the basement membrane ; when the odontoblasts differentiate they largely sever those connections but a few fibres are always to be found passing from the substance of the dentine between the odontoblasts to join up with the persisting network in the pulp.

In the formation of the tooth the first stage is represented by a red granulation of obscure significance between i.d.e. and pulp within the depths of the cup. This is replaced by a very thin layer of collagen which for a brief period during this initial stage has the simple domed shape of the original cup ; almost at once however a reshaping of the i.d.e. occurs into its later bicuspid form. Collagen is added below the developing cusps, so that for a time they appear as separate crests with a thinner zone between, later collagen is added to the whole inner surface and extends downwards laterally to build up a homogeneous tissue in the characteristic shape of the top of the tooth. The subsequent appearance of tubules in this tissue shows it to be dentine. Before this dentine is sufficiently thick for the tubules to have become defined, but when quite sufficiently thick to outline clearly the top of the tooth, a histologically quite different substance appears on its outer surface (Pl. 2, fig. 6), which seems without doubt to be an ectodermal enamel being laid down on the dentine surface. The deposition of this enamel framework and its subsequent calcification occupy only a relatively very short period of development, judged by the correspondingly slight growth in thickness of the dentine, but stages can be found of intermediate thickness. Histologically the layer at no time gives a collagen reaction, being pink with trichrome and strongly red with azan ; when present at all it is always sharply differentiated from the underlying dentine, and no evidence was found suggesting that it could represent the conversion of a first formed outer layer, previously indistinguishable from the dentine, rather than a secondary formation of a different type. Considerable attention was devoted to checking this interpretation, owing to Kvam's (1946) suggestion that in some newts (*Triton cristatus* and *punctatus*) the enamel is mesodermal in origin. The precise nature of the ground substance of the enamel however could not be determined ; specific keratin stains, relying upon the presence of sulphur, gave occasionally positive but generally indeterminate reactions, although the low sulphur content of amphibian keratin reduces the significance of these results, and the strong azan reaction indicates the probability of keratin. The ground substance itself rapidly disappears as its calcification proceeds and in sections of later stages only an enamel space remains.

Changes in the i.d.e. cells show much the same sequence of changes as in teleosts ; a regular columnar form is assumed as the mesoderm concentrates, an initial hypertrophy accompanies the formation of the early dentine, followed by a more pronounced hypertrophy which reaches a maximum as the enamel framework appears and calcifies, finally there is a slow and somewhat variable

reduction of the cells. The second hypertrophy passes down over the dentine below as a much reduced wave. The dentine itself is built up laterally and internally, its structure showing up best with silver impregnation. Rather coarse longitudinal fibres are common and at all levels fibres pass inwards between the odontoblasts to join up with the open reticular network of the pulp, but the bulk of the tissue consists of a close intermingling feltwork of finer fibres. Dentinal tubules are numerous, especially towards the apex of the pulp, and here they frequently join up at their bases to form larger tubes, with a corresponding concentration of the odontoblast processes. Several processes from the one odontoblast, either initially fused or arising separately, is a feature of these cells in urodeles. The odontoblasts themselves are large and fairly regularly arranged in a single layer during tooth development, in the mature tooth they become much reduced and somewhat irregular but even in functional teeth a few at least of their processes appear to persist.

Growth in length of the tooth and its transference to its final position involve an elaborate series of interactions in the soft tissues. An initial feature, which it may be useful to emphasise, is that the inner end of the tooth does not push down any deeper into the dermis during development, as it does in teleosts. In other words increase in length, although it still occurs at the inner end of the tooth, results only in the outward movement of the tip of the tooth towards the surface (Pl. 2, figs. 6 & 7). At the stage when the enamel organ first assumes its cup-like shape its x.d.e. on the labial aspect is a simple extension of the labial wall of the dental lamina. However the x.d.e. comes to thin off and to fold slightly over the apex of the i.d.e. before becoming continuous with the laminar wall, and these features tend to obscure the important point that the developing tooth with its covering of i.d.e. is in reality pushing up the centre of the lamina, hence always surrounded by ectoderm cells and ultimately reaching the surface without any penetration of the basement membrane. Such a process would leave the tooth enclosed within the two walls of the lamina were it not that an intucking makes its appearance from below, at about the same time as the tooth substance begins to appear, which both establishes an x.d.e. proper all round the deeper end of the enamel organ and also separates the base of the enamel organ from the inner end of the lamina (Fig. 2B). This intucking deepens with the growth of the tooth, so that in effect a zone of attachment moves up the labial side of the lamina, with an increase of x.d.e. and a progressive freeing of the lamina from its inner end. When the intucking eventually reaches the level of the basal epidermis then lamina and dental unit part company. By this stage the tooth has already penetrated into the superficial epidermis, its tip still enclosed by its i.d.e. but its x.d.e. turning off into the basal layer.

Meanwhile it is necessary to return to an earlier stage when the tooth tip has reached about two thirds up the lamina, because at this stage the length of the young tooth appears to be increasing beyond that of an adult tooth macerated off the jaw. Actually this is due to the beginning of pedicel formation, but until calcification begins in the pedicel the fibrous junction between the two is not easily distinguished, the junction itself being simply a continuation of the longitudinal fibres of the tooth without the finer series of consolidating

fibres. The close integration of tooth and pedicel is further emphasised by the dental epithelia extending down the outer face of the latter, in the same relationship as they bear to the tooth, and the odontoblast layer extending similarly down its inner face. The pedicel therefore, although it contains no tubules, must be looked upon as in some sense a dentinal rather than an osseous structure. In sections cut transverse to the line of the jaw the lingual wall of the pedicel can be seen to lengthen to a very much greater extent than does the labial ; moreover the inner end of the former continues to maintain the same relative position in the dermis as did the base of the tooth, so that the tip of the tooth continues to be pushed outwards into the epidermis. Eventually the whole dental unit separates off from the lamina (Pl. 2, fig. 7), and pedicel formation is completed during the passage of the unit labially through the soft tissues to its final position against the bony flange. Also completed is the eruption of the tooth till its tip, still covered with flattened i.d.e. cells, protrudes just beyond the epidermal surface, though in usage later the soft tissues are further pressed down. The degree of eruption is governed by the growth of the pedicel, so that the same mechanism could function equally in forms where the teeth project much further from the jaw than in the salamander, but in all cases eruption must be completed before the fusion of pedicel and flange takes place. The explanation of the asymmetrical growth of the pedicel is that only its upper end, above the level of attachment to the bony flange, forms as a complete tube ; below only about two-thirds of the wall is a genuinely new formation and it is the free edges of this portion which fuse with the flange. As a a result the labial wall of the pedicel throughout most of its length is really composed of the bony tissue of the flange. During development the pedicel proper can be distinguished by its covering of dental epithelia, at maturity these flatten out and the sheet shrinks but the pedicel tissue can still be distinguished from the flange tissue by its lack of enclosed bone cells. The tooth to pedicel junction resembles that of the hellbender, where it will be described.

In the smooth newt conditions are closely similar to the preceding.

(c) *Teeth of the hellbender*

If a piece of whole jaw is lightly stained in alizarine and cleared in glycerine the teeth can easily be dissected out and a close series examined during the early critical stages. Calcification appears in the superficial dentine of the apical cusp and spreads down the tooth, joining up with a second centre which appears later in the labial cusp ; about the stage when these two expanding centres meet the enamel can be seen, again appearing first on the apical cusp and later on the labial, as a layer which increases in thickness and extends down the sides of the tooth. At first it stains lightly pink but as its calcification increases it becomes shiny, transparent and non-staining ; its greatest thickness is on the crests of the cusp ridges, thinning abruptly lingually and more gradually labially, so that its deposition is accompanied by minor changes in the shape of the tooth tip. In the case of the labial cusp this results in a noticeably more truncated appearance to the crest of the ridge than it possessed when formed of dentine alone ; and in the apical cusp of an increase in the breadth of the tooth, with a slight constriction where the enamel layer ends.

Such shape changes can hardly be explained unless the enamel is being deposited from the outside. These early stages can be sectioned undecalcified with some success, embedded in celloidin and orientated on pieces of liver, and histological appearances compared with whole mounts. In both cases there appears to be no doubt that the enamel is of ectodermal type. Quite a strong yellow tint appears in the enamel, but only after calcification is far advanced.

In sections of hellbender jaws the relationships have a general similarity to those of the salamander. The most striking difference is that the dental unit separates off from the lamina, although of course continuing to maintain an epithelial connecting strand to the epidermis, at a relatively much earlier stage. As a result the replacement unit is far from fully formed when it takes up its position in the base of its predecessor's pedicel, and erosion of the latter might in this case be associated directly with its growth. The attachment of the functional tooth to its pedicel is similar and the larger size of the structures allows the mechanism of tooth movement to be more readily understood. From its resting position, determined by the surrounding soft tissues, the tooth can pivot about an axis in the line of the jaw. Under pressure towards the buccal cavity the inner base of the tooth swings inside the corresponding lingual lip of the pedicel, the junction fibres doubling on themselves, so that a considerable range of movement is possible in this direction ; outward movement on the other hand is arrested almost at once by the flat labial faces on tooth and pedicel coming into direct contact and the inner junction fibres coming under tension.

(d) *Larval teeth*

The simple monocuspid teeth which occur normally in urodeles before metamorphosis offer the same great advantage for the observation of enamel formation as do the similarly shaped teeth of teleosts. For here again the enamel tip is pointed whereas the dentine apex on which it is based is rounded, so that the shape itself of the first tooth tissue to appear can be used, in addition to any histological differences, as evidence of its nature. In larval salamanders and newts however these teeth are rather small, so use instead has been made of the axolotl.

The teeth of the axolotl are arranged in two series in each half jaw, with their replacements disposed lingually ; an outer series as a single regular row along the edges of the jaws, on premaxilla and maxilla above and dentary below, and a less regular inner series, on prevomer and palatine above and splenial below. In specimens of about 15 cms. in length, such as were mainly used, the majority of teeth in the outer series are bicuspid and in the inner monocuspid, with a higher proportion of monocuspids in smaller specimens. The change over from the one form to the other is not a regular process, since the replacement for a monocuspid may be a bicuspid and vice versa, and both develop from the same dental lamina. In the development of the bicuspids the dentine appears first and is later covered by an ectodermal enamel in the manner described for the salamander, the enamel matrix differing only in its less marked affinity for azan or indeed any other stain, so these bicuspids can perhaps best be looked upon as adult teeth appearing precociously. The

presence of a yellow colour in the i.d.e. cells and in the enamel to be described shortly in monocuspids is similar in bicuspids except that their enamel is yellow from its first appearance, the colour however is lighter and only noticeable in whole teeth. Disintegration of the bicuspid enamel with acid also is much more rapidly brought about than in mature monocuspids.

For monocuspids then the inner series of teeth were used, first with the alizarine-glycerin technique for a general view and to facilitate removal of individual teeth. In cleared material the arrangement of the teeth is seen as a long row along the bone and short rows at right angles ; the latter represent replacement sequences which at their maximum consist of a shed tip still embedded in the epidermis labially, an attached functional tooth, a partly formed replacement tooth and a very early stage with the tooth substance not yet calcified. Replacement is too irregular to be described as alternating, and there is a marked variation in the orientation of the early teeth. The two most striking features of teeth dissected out individually is first that the earliest stage obtainable still has a pointed tip and second that this tip becomes increasingly tinted by a yellow colour apparently passing into it from the soft tissues. The colour appears in the i.d.e. cells quite shortly after the formation of a new unit has begun, as can be well seen in material freshly fixed in alcohol before clearing. Later the yellow colour begins to show in the originally colourless tip of the tooth, but becomes strong only after calcification is well advanced and when the distinction between dentine and enamel is sufficient to show that the colour is affecting the latter only. Roughly parallel changes occur in the reaction of the enamel to weak (5 per cent) nitric acid. Before calcification the enamel framework remains unaffected, as calcification progresses the framework increasingly loses its coherence and becomes shrunken and distorted under the influence of the acid until finally it virtually disappears, to leave the tooth represented merely by a dome of early dentine. However as the yellow colour becomes pronounced the enamel begins to take on a secondary coherence and in later stages the initial effect of the acid is simply to shrink the enamel cone somewhat and loosen it from the dentine ; only after prolonged acid treatment does this yellow matrix finally disintegrate. These observations on whole teeth corroborate phenomena which can now be described in more detail from sections.

The accurate determination of the shape of the earliest tooth substance can clearly go far to decide whether this enamel is of ectodermal or mesodermal type. The alternative to be decided however—whether the substance is at first dome-shaped and so probably dentine, or pointed and so probably mesodermal enamel—requires that the plane of sectioning should coincide very closely with the long axis of the tooth, since with such small structures even a slight obliquity may give a misleadingly rounded appearance to the top of what is really a cone. The small size of the early tooth units makes separate removal and accurate orientation on pieces of liver impracticable, while on the other hand precise orientation of a whole piece of tissue is of limited value because of the variation in the orientation of the early teeth themselves, with the minor complication that the rows of teeth are curved. Large numbers of serial sections were cut therefore, transversely to the tooth rows, and in their examination

a pointed tooth was taken as discounting any doubtfully domed tooth of comparable age. On this basis a close series of stages was built up to cover the critical phases of early development. The enamel organ is initially cup-shaped, as in bicuspid teeth, and the i.d.e. again reshapes itself as the tooth substance appears, but in this case it takes the form of a simple cone so that the tooth is monocuspid from the beginning (Pl. 2, fig. 2). The tip of the tooth builds up progressively into a cone similar in size and shape to the enamel tip of the mature tooth, before the first dentine fibres appear across its dome-shaped inner end ; so there appears to be no doubt here that the enamel is developing before the dentine and is of mesodermal type. The uncalcified matrix of the enamel appears more or less homogeneous and takes collagen stains, although less strongly than does the dentine ; since it is the first to form also the basement membrane is incorporated into its surface before that of the dentine. The further feature of mesodermal enamel, namely cytoplasmic processes from the pre-odontoblast cells, appears to be absent ; these cells are squarely arranged against the inner matrix surface during its development and appear responsible for its formation but at no stage have processes from their ends been detected. Really fine strands of cytoplasm would certainly be difficult to demonstrate, but it is noticeable that the odontoblast processes which develop later into the dentine are very clearly visible, more so with colour contrast than in monochrome (Pl. 2, fig. 3). Moreover a narrow zone of homogeneous dentine is already laid down before the terminal branches of the dentinal tubules and their contained processes make their appearance, so that a genuine absence of processes from earlier stages appears probable. As in salamanders several processes may originate from a single odontoblast, and here the processes certainly persist in mature teeth (Pl. 2, fig. 5). Further development of dentine and pedicel resembles that already described, although the latter are relatively smaller.

The onset of calcification can be determined from sections of early teeth removed from alcohol-fixed tissue and attached to pieces of liver ; alizarine staining shows that the reaction appears first in the enamel, and at the stage when the earliest dentine is beginning to form. Calcification proceeds rapidly, so that by the time an appreciable band of dentine is present, itself calcifying from its boundary with the enamel, the enamel is becoming refractory to the stain and too brittle to section. In ordinary decalcified sections the first sign of calcification in the matrix is a tendency to shrinkage, followed by an increasing tendency to disintegration so that, after passing through a brief PAS-positive phase, there is a period in development when the decalcified matrix is represented in sections merely by indefinite remains or is entirely absent (Pl. 2, fig. 3). Once again the dentine is entirely unaffected by whatever process removes the enamel matrix, despite the histological similarity of the two tissues. This stage might possibly be misinterpreted as the beginning of tooth formation, with the dentine therefore appearing first, but even when using sections alone such an impression would be corrected by the arrangement of the upper i.d.e. cells to enclose an enamel space. Quite shortly the secondary coherence becomes manifest in the enamel matrix (Pl. 2, fig. 4) and is retained subsequently, so that a cone of decalcified enamel can still be found on the

erupted tooth (Pl. 2, fig. 5). In practice these cones are frequently missing however, slight shrinkage tending to loosen their attachment to the dentine. The yellow colour of the i.d.e. cells which is visible in whole mounts cannot be seen in sections, but it does appear in the secondary enamel framework where it is made more apparent by the latter's lack of any marked staining affinity. The substance responsible for the secondary coherence appears most likely to pass into the enamel from the i.d.e. cells, certainly the transference of the colour itself implies the existence of a functional route for the passage of material from ectoderm to enamel.

DISCUSSION

The similarities between the teeth of different vertebrates are so considerable and frequently so striking that at first all seem to fit very satisfactorily into a single homologous framework. An enamel organ, derived initially from the basal cell layer of the epidermis and very consistent in its general appearance, envelopes the outer face of the tooth in two layers of epithelium, and similarly a central mesodermal pulp forms a single layer of odontoblasts on the inner face ; the main column of the tooth is formed of dentine, typically permeated by dentinal tubules and always represented by a dense collagenous framework when the hardening salts are removed with acid ; finally the functional top of the tooth is normally covered by a much harder layer which breaks down completely with acid treatment. Most divergencies from this plan appear of minor importance : for example the suppression of the dentinal tubules or of the hard outer layer, the essentially separate origin of the dental units in some classes and their derivation from dental laminae in others, the extent to which a cellular meshwork develops between the two epithelia of the enamel organ and so on. What appears to be a fundamental difference however does make its appearance in the method of formation of the hard outer covering, and as an incidental result has caused some difficulty in terminology. In reptiles and mammals this covering only begins to form after the first dentine has appeared, is later built up in contact with ectodermal cells only, and amongst various other differencies its organic framework is of a keratinous nature ; whilst in elasmobranchs and teleosts the covering appears, and is indeed fully formed, before the dentine begins to develop at all, it forms internally to the basement membrane in contact with the pulp cells and appears therefore to be primarily at least of mesodermal origin, and its framework is of a collagenous nature. In the latter case the fact that the outer covering appears first, may contain cytoplasmic processes and differs in other ways from the enamel of higher types does give some grounds for its designation as a form of dentine (durodentine, hyalodentine) however it differs equally markedly, particularly in the lack of the closely knit organic framework unaffected by acid which is so characteristic of all forms of dentine, and a further objection to this nomenclature is the impractibility of determining the origin of the layer in fossil material. It appears less confusing therefore to call this outer layer enamel in all cases and, where evidence permits, to qualify it further as true or ectodermal enamel on the one hand and mesodermal enamel (Kvam, 1946) on the other. The mesodermal enamel of teleosts differs from that of

elasmobranchs (Kerr, 1955) in possessing a greater proportion of discrete collagenous fibres in its uncalcified matrix and in some minor points but is sufficiently similar for a common origin to be envisaged. In the urodeles however the enamels of the larval monocuspid and of the adult bicuspid teeth are themselves different. In the latter it is of ectodermal type, unusual in that it is laid down during a very brief period of development but typical in only appearing after the earliest dentine has formed, and its organic framework is probably keratinous ; appearances indeed are very similar to those described for the bullfrog by Gillette (1955). In the monocuspid teeth on the other hand the enamel is of mesodermal type, appearing before the dentine and having a collagenous framework. The presence of both types of enamel in the same organism at different stages of its development suggests that a replacement of mesodermal by ectodermal enamel could have occurred during tetrapod evolution, and the possibility that the one type can be converted into the other must be examined. In this connection the yellow pigment which appears first in the epithelial cells and later in the originally colourless monocuspid enamel appears to indicate that the passage of substances from the ectoderm into mesodermal enamel can occur, and this is supported by the development of the secondary coherence in the enamel after an appreciable amount of dentine separates it from the pulp. Once such a passageway is established the replacement of mesodermal by ectodermal enamel becomes possible, but here further work is required.

The teeth are attached to the underlying bone by calcified tissues of rather uncertain status, which form moreover in a sufficiently different manner in teleosts and urodeles to imply a different evolutionary origin. In the fish the inner end of the enamel organ stops at the inner end of the tooth proper and their bone of attachment is formed in association with an extension of the odontoblast layer only, whereas the urodele pedicel is formed in association with both tissues. Further differences show in the growth and eruption of the teeth. In both the increase in length of the tooth results from the addition of new dentine at its inner end but while in teleosts this causes the inner end of the tooth to extend deeper into the dermis, where such extension can occur unimpeded, in the urodele the tooth tip moves upwards from the first as the tooth grows and the inner end of first the tooth and then the pedicel never extends deeper into the dermis than its original position at the inner end of the dental lamina. Hence eruption of the teleost tooth appears to be a reaction to the underlying bone and the developing bone of attachment, depending for its initiation primarily upon the thickness of the dermis, and that of the urodele tooth to be a continuous process from its first appearance and independent of those factors. In the former eruption occurs through the persistent epithelial strand and in the latter virtually up the centre of the dental lamina, so that in neither case does the tip of the tooth pierce the basement membrane.

SUMMARY

1. The formation of the enamel has been investigated in a number of teleosts and primitive actinopterygians and found to be of a mesodermal type with considerable similarity to that of elasmobranchs. The structure of the

dentine, the eruption of the teeth and their method of attachment to the underlying bones have also been described.

2. A comparable study has been made of some urodele teeth, in both adult and larval forms. In the former the teeth are bicuspid and the enamel ectodermal, in the latter they are monocuspid and the enamel mesodermal.

3. A comparison has been made between the structure, attachment and method of eruption of the teeth in the two classes, and the possible relationship of the two types of enamel has been discussed.

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ADDITIONAL NOTE

The yellow colouration of the enamel appears to be due to haematite (ferric oxide, Fe_2O_3) presumably hydrated (Schmidt, W. J., *Z. Zellforsch.* **49,** 46 (1958) and *Zool. Anz.* **161**, 168 (1958). For monocuspid axolotl teeth see also Levi (1939).

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EXPLANATION OF THE PLATES

Plate 1

Fig. 1.—*Polypterus* jaw tooth, early stage. Pre-enamel partly calcified but cortical and process fibres still present, dentine beginning to form ; numerous cells present between epithelia of enamel organ. Trichrome. Scale 75 μ.

Fig. 2.—Eel jaw teeth, two stages. Older tooth being phagocytosed from base and with enamel absent, replacement tooth formed of shrunken pre-enamel and early dentine. Trichrome. Scale 150 μ.

„ 3.—Gurnard jaw tooth, very early stage. H. & E. Scale 100 μ.

„ 4.—As last, later stage with first appearance of pre-enamel. H. & E. Scale 100 μ.

„ 5.—Whiting branchial tooth, early stage. Pre-enamel shrunk, epithelial process convoluted. Trichrome. Scale 75 μ.

„ 6.—Plaice jaw tooth. Calcification of pre-enamel. Dahl. Scale 100 μ.

„ 7.—Cod jaw tooth. Lateral section of junction of tooth to bone of attachment. Gomori. Scale 75 μ.

PLATE 2.

Fig. 1.—Axolotl dentary. Inner view of bone of jaw with pedicels and one detached bicuspid tooth. Alizarine. Scale 250 μ.

„ 2.—Axolotl splenial monocuspid tooth, very early stage. Pointed cone of pre-enamel Trichrome. Scale 25 μ.

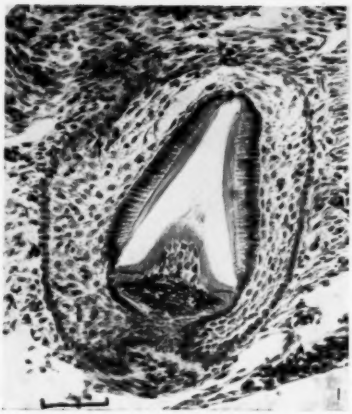
„ 3.—As last, later stage. Dentine only present. Trichrome. Scale 50 μ.

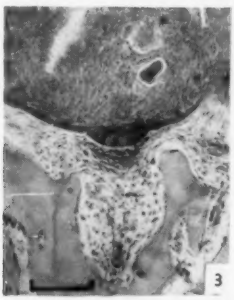
„ 4.—As last, later stage. Secondary cohesion appearing in enamel. Trichrome. Scale 50 μ.

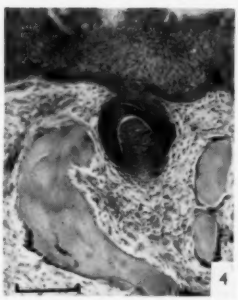
„ 5.—As last, later stage. Erupted tooth with enamel cone present. Trichrome. Scale 50 μ.

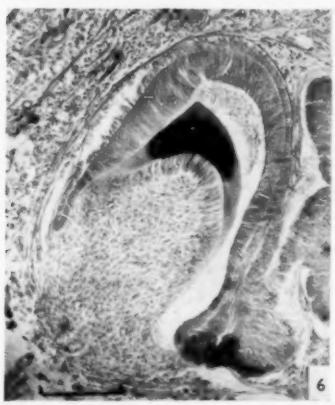
„ 6.—Salamander jaw tooth, early stage. Darker enamel layer just formed on dentine. Trichrome. Scale 50 μ.

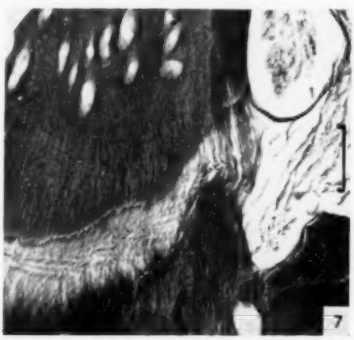
„ 7.—As last, tooth about half-formed. Pedicel development established, tooth free of dental lamina but not yet attached to bone of jaw. Edge of jaw to right. Trichrome. Scale 100 μ.



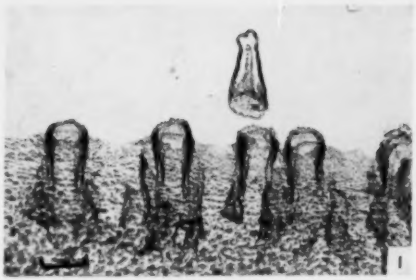


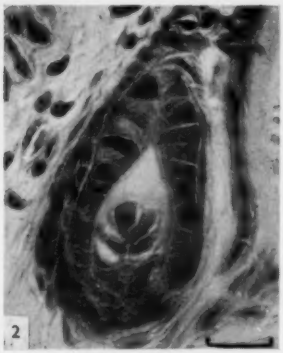


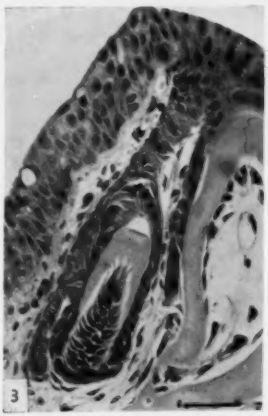


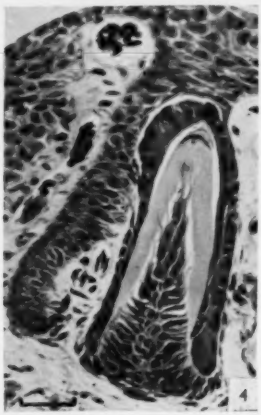


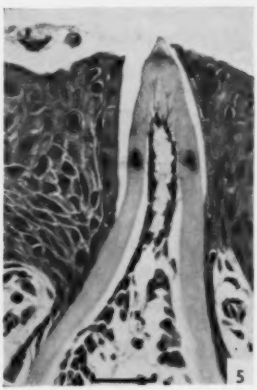
Development and structure of some actinopterygian and urodele teeth.

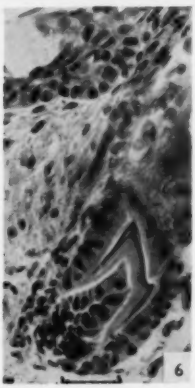


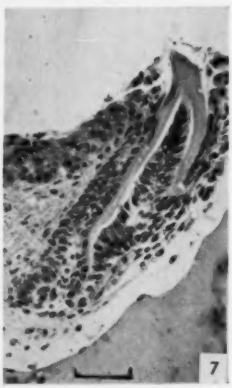












Development and structure of some actinopterygian and urodele teeth.

THREE SPECIES OF KAMPTOZOA NEW TO BRITAIN

BY

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(With 1 plate and 3 figures in the text)

CONTENTS

	Page
Introduction	423
Loxosomella kefersteinii (Claparède), 1867	423
Loxosomella antedonis Mortensen, 1911	425
The seasonal occurrence of *L. kefersteinii* and *L. antedonis* in Swansea Docks	427
The formation, release and behaviour of buds of *L. kefersteinii* and *L. antedonis*	429
Loxosoma annelidicola (van Beneden & Hesse), 1864	430
Summary	431
Acknowledgments	432
References	432
Explanation of plate	433

INTRODUCTION

Three species of Kamptozoa (=Entoprocta), all belonging to the family Loxosomatidae, have been recently recorded for the first time in British waters. These have been identified as *Loxosomella kefersteinii* (Claparède), *L. antedonis* Mortensen and *Loxosoma annelidicola* (van Beneden & Hesse). The two species of *Loxosomella* have been found abundantly, though at different times of the year, on test surfaces immersed in the Queen's Dock, Swansea. Observations have been made on the formation and liberation of the asexually produced buds, and on their powers of locomotion which appear responsible for facilitating dispersal and the colonization of suitable submerged objects.

LOXOSOMELLA KEFERSTEINII (Claparède), 1867

In October 1956 a few individuals of a species of *Loxosomella* were found attached to a colony of *Bugula* from Swansea docks. A large number of specimens was subsequently found during the late summer of both 1957 and 1958 on panels being used for the study of settlement and fouling in the docks. The species was identified as *L. kefersteinii* from the account given by Prenant & Bobin (1956, p. 68).

The most striking character shown by these specimens is the manner in which the buds are attached (Fig. 1 b ; Pl. 1, fig. 1 c). Up to four have been found on either side of the calyx, attached, not by the base of the peduncle, but by an umbilicus arising just below the calyx of the bud ; the peduncle is therefore free and projects upwards. Three species of *Loxosomella* with this method of budding are known, and it has been suggested (Mortensen, 1911 ;

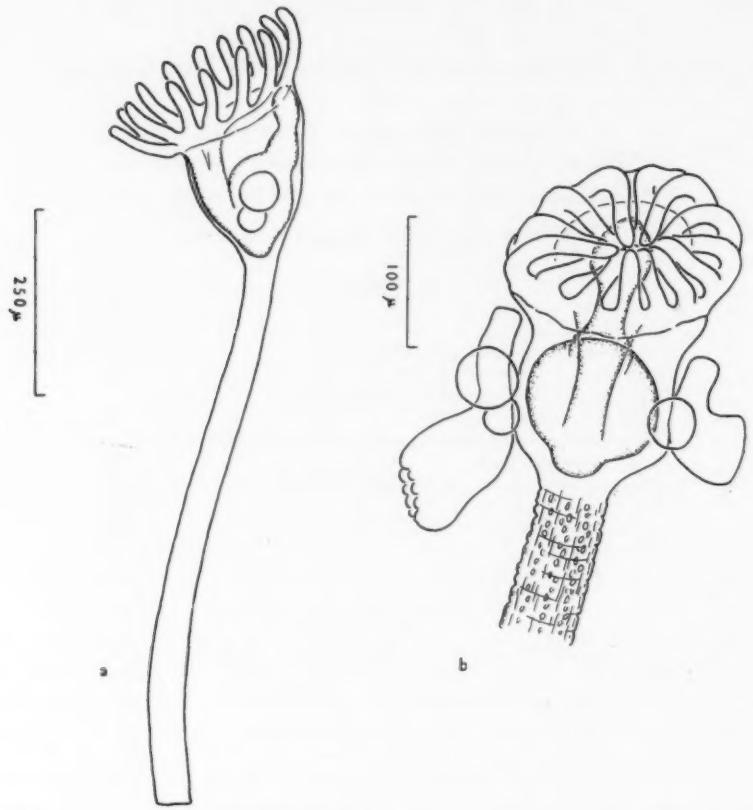

Fig. 1.—*Loxosomella kefersteinii*. (a) Side view of complete individual. (b) Frontal view of calyx of another specimen showing the mode of attachment of the buds.

Bobin & Prenant, 1954 ; Marcus, 1957) that a separate genus might be created to contain them. The first, *L. annulata* (Harmer, 1915), is a rather small species, not more than 750 μ long, in which the peduncle constitutes one half to three quarters of the total length. It has nine, rarely eleven, tentacles. The buds never number more than two and are restricted to one side of the calyx. The second, *L. mespe* du B.–R. Marcus (1957), is also small, not exceeding 650 μ in length, the peduncle being about as long as the calyx. The tentacle number is twelve to fifteen, barely different from that of *L. kefersteinii*, but never more than one bud is present on each side of the calyx. The third species, *L. kefersteinii*, is larger and according to Prenant & Bobin often reaches 1·5 or even 2 mm. in length. It has eleven to fourteen tentacles, and up to six buds may be present on each side of the calyx.

The Swansea specimens agreed with the description of *L. kefersteinii* in regard to the numbers of tentacles and buds, but were smaller in size (Table 1). The majority measured about 1 mm. in length although a few larger individuals were found. The calyx in well-developed specimens was about 300 μ long, but only 160–200 μ in smaller individuals—well below the figure of 500 μ quoted by Prenant & Bobin. The peduncle was usually about three times the length of the calyx (Fig. 1 a ; Pl. 1, fig. 1). This is longer than previously recorded and approaches the proportions of *L. phascolosomatum* (Vogt), although the two species can readily be separated on other characters, including the mode of budding. *L. phascolosomatum*, which lives attached to various species of *Phascolosoma*, reaches a size of 2·5 mm. The lophophore, which is not oblique as in *L. kefersteinii*, bears twelve to eighteen tentacles.

The differences from the description given by Prenant & Bobin (1956) do not seem to us to be of great importance, and we have no hesitation in referring our specimens to *L. kefersteinii*. Moreover the identification has been confirmed by Mlle Bobin. It is, however, important to note that the peduncle of this species can exceed twice the length of the calyx, since the opposite is stated by Prenant & Bobin in their key to species (p. 59).

TABLE 1

Measurements of 100 individuals each of *Loxosomella kefersteinii* and *L. antedonis* taken from panels immersed in Swansea Dock July–August, 1958.

	L. kefersteinii	*L. antedonis*
Average total length	1·06 mm.	0·41 mm.
Maximum recorded length	1·60 mm.	0·57 mm.
Average calyx length	0·27 mm.	0·21 mm.
Maximum recorded calyx length	0·33 mm.	0·29 mm.
Minimum recorded calyx length	0·16 mm.	0·12 mm.
Average stalk length	0·79 mm.	0·21 mm.
Ratio stalk : calyx (average)	2·9	1·0
Ratio stalk : calyx (maximum)	4·5	1·7
Ratio stalk : calyx (minimum)	1·8	0·6

LOXOSOMELLA ANTEDONIS Mortensen, 1911

L. antedonis was first noticed in the spring of 1958 on settlement panels from Swansea. Compared with *L. kefersteinii* the most obvious feature was the shortness of the peduncle ; closer examination revealed the fundamental difference in the type of budding. None of the species described by Prenant & Bobin (1956) agreed fully with the Swansea specimens from which the following description was prepared.

The species (Fig. 2) is a small one, averaging about 400 μ in length, with the peduncle being generally about the same length as the calyx (Table 1). The bud has a well-developed pedal gland (Fig. 2 a) but this atrophies after liberation, and no trace of the gland can be seen in the adult (Pl. 1, fig. 2 b). No pedal disc is present. The peduncle passes into the calyx without any clear line of demarcation. The lophophore is oblique and bears fourteen, rarely sixteen, tentacles, with a wide space in the midline between the posterior pair. When fully open the tentacles have a span of 450–600 μ—greater than the animal's total length (Pl. 1, fig. 2 b). When seen from the front the stomach

is trilobed, sometimes strongly so. The budding zone is fronto-lateral, and buds seem to form more or less alternately on each side (Pl. 1, fig. 2 a) ; a total of up to five may be present. The bud has a very distinct foot along which runs the duct of the pedal gland ; the gland itself extends up the peduncle almost to the base of the stomach (Fig. 2 a). Buds reach a length of about

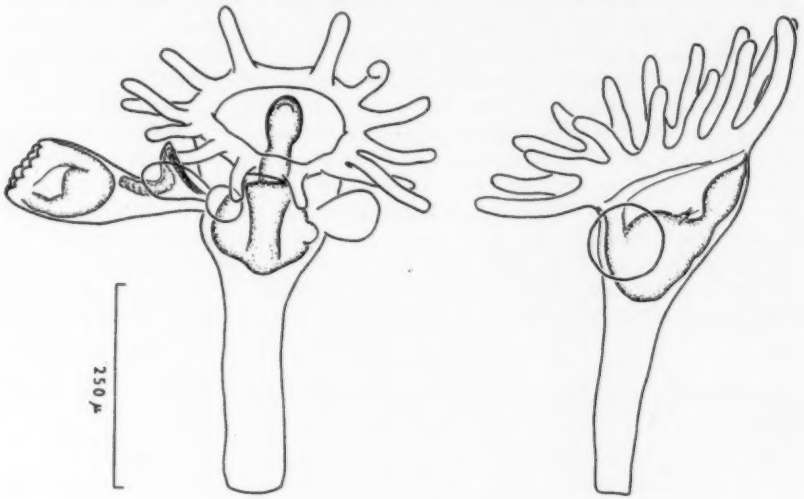

Fig. 2.—*Loxosomella atendonis*. (a) Frontal view. The largest bud shows a well-developed pedal gland. (b) Lateral view of a smaller specimen showing the size and position of the sense organ.

300 μ before liberation and have twelve tentacles. They may even be forming their own buds while still attached to the parent. A prominent sensory papilla is present just behind the budding zone level with the top of the stomach (Fig. 2 b) ; it cannot be seen from the front when the tentacles are fully extended, but may be seen when they are withdrawn or in lateral view. Sometimes it is quite impossible to locate these organs which are therefore presumably retractile. The species shows a characteristic avoiding reaction bending parallel to the substratum with the lophophore closed and facing downwards.

L. antedonis described by Mortensen (1911) from the Greenland Sea (77°N, 17½°W) agrees very closely with the present form in nearly all its characters. Mortensen's description, made on preserved material, is as follows : " The calyx is beautifully oval, without expansions on the sides ; it passes very gradually into the stalk, which is simply cylindrical, slightly narrowing towards the base. The length of the stalk is somewhat variable, from a little shorter to a little longer than the length of the calyx. The total length of the animal is 0·5–1 mm. Generally the stalk is curved, the animal bending its atrial opening

toward the cirrus [of the crinoid] to which it is attached. The number of the tentacles is fourteen or sixteen. The stalk does not contain any foot gland, while in the buds there is a distinct gland. This gland after having secreted a finely granular substance, by which the animal fixes itself, atrophies completely so as to leave no trace at all in grown specimens ". The figures show the base of the peduncle to be slightly expanded but there is no pedal disc, although the attachment substance spreads out around the base and accumulates debris. Mortensen's Greenland specimens therefore agree very closely with those from Swansea, although somewhat larger. The number of tentacles is the same, and they agree in showing prominent sense organs. Very little is known about the extent of variation in species of *Loxosomella*, and the slight difference in size between the specimens from the two localities would not seem to be a character of sufficient importance to be the distinguishing feature of a new species. It should, however, be borne in mind that Mortensen's specimens came from 300 fm. in Arctic waters on the crinoid *Poliometra prolixa* (Sladen), whereas the present material comes from panels submerged near the surface of a warm water dock (see below).

In appearance *L. antedonis* is somewhat similar to *L. claviformis* (Hincks), (Atkins, 1932 ; Prenant & Bobin, 1956). The latter usually measures about 0·7–1·0 mm. in length, the peduncle being as long or somewhat longer than the calyx. The tentacle number is ten to twelve, rarely fourteen, and eight in mature attached buds ; *L. antedonis* has a greater number of tentacles, especially in the mature bud. The sense organs of *L. antedonis* are more prominent than in *L. claviformis* (Atkins, 1932, Fig. 6B). A pedal disc is present in *L. claviformis*. *L. antedonis* would therefore seem quite distinct from *L. claviformis*, and the Swansea specimens appear to be referable to the former.

THE SEASONAL OCCURRENCE OF *L. KEFERSTEINII* AND *L. ANTEDONIS* IN SWANSEA DOCKS

Both species of *Loxosomella*, as is normal in the genus, have previously been recorded as epizoic : *L. kefersteinii* on hydroids or Polyzoa (Prenant & Bobin, 1956), and *L. antedonis* on a crinoid (Mortensen, 1911). The abundant occurrence of these species on specially roughened surfaces of ' Tufnol ' plates (composed of non-toxic phenol-formaldehyde resin) is therefore rather surprising. Although daughter zoids spread over other organisms growing on these panels, the original settlement and the greatest numbers of both species always occurred on the panel surface.

The fauna accompanying the species of *Loxosomella* on the panels includes native species such as *Hydroides norvegica* (Gunn.), *Ciona intestinalis* (L.), *Diplosoma listerianum* (Milne Edwards) and a species of *Bugula*, together with a number of immigrant organisms such as *Balanus amphitrite* var. *denticulata* Broch (Crisp & Molesworth, 1950), *Merceriella enigmatica* Fauvel and *Bugula neritina* (L.) (Naylor, 1959). The latter are all warm water forms and it is significant that the water in the dock is maintained at a temperature some 7–10°C above that of the sea as a result of the entry of a warm water effluent from the Tir John Power Station. In January 1946, for example,

the effluent had an average temperature of 18°C which dropped to 12°C in the dock itself, while the sea outside was at 5°C. In 1957 a minimum temperature of 14°C was recorded in February and the summer maximum was just over 26°C (Naylor, 1959). The temperatures in the dock therefore range between about 12–14°C in winter and 26–27°C in summer.

L. kefersteinii has previously been recorded from the Red Sea, the Adriatic and the Mediterranean and has probably been carried to Swansea on oil tankers coming from those waters. Naylor (1957) has shown that the grapsoid crab, *Brachynotus sexdentatus* (Risso), recently introduced to the dock, is also characteristic of the eastern Mediterranean and the Red Sea. The high temperature of the water in the Queen's Dock, where the oil tankers berth, no doubt accounts for the growth and multiplication of these exotic species.

The kamptozoans are most easily observed on panels which have been immersed for two weeks. On these both young and fairly well developed specimens are evenly distributed over the surface. In this time individuals of both species can produce buds ; the larger specimens of *L. antedonis*, for example, bearing two buds on each side. In their ability to colonize newly immersed test surfaces and in their rapid maturation these species resemble other small or microscopic forms such as *Barentsia gracilis* (M. Sars) and species of *Zoothamnion*, *Folliculina* and *Schizosiphon*. On panels immersed for a month species of *Loxosomella* are often smothered out to some extent by other forms, such as barnacles, ascidians and tube builders, but where they occur they form dense patches of well developed individuals often budding profusely. On panels immersed for six weeks to four months more individuals may be found growing on other animals, such as empty or occupied barnacle shells, *Ciona intestinalis* and *Ascidiella aspersa* (O. F. Müller), as the Tufnol surface becomes increasingly covered by the more dominant forms. In the conditions prevailing in the dock the individuals of both species of *Loxosomella* reached their maximum size in two to three weeks, and are thought to live and produce buds for at least eight to ten weeks.

L. kefersteinii was first noted on the panels in early July 1957 and continued to settle until the end of the year, with a peak in September and October and a reduction of numbers from late November until its disappearance in December. However, from July to early September the species, together with many other small delicate forms such as *Nolella pusilla* (Hincks), *Bowerbankia caudata* (Hincks) and *Barentsia gracilis*, was largely excluded or obscured by the dense, rapidly developed cover of mud tubes belonging to *Polydora ciliata* (Johnston) and *Corophium acherusicum* A. Costa, and to some extent also by large specimens of *Ciona intestinalis*. The increase in numbers of *L. kefersteinii* up to 150–500 per 100 cm² in September and October 1957 may therefore be only an apparent one. Later in the autumn the settlement of most of the associated species, especially of *C. intestinalis* and *Balanus amphitrite*, ceased, and from mid November it consisted only of very small quantities of *Botrylloides leachi* (Savigny) and *Diplosoma listerianum* with small numbers of *L. kefersteinii*. In 1958 *L. kefersteinii* again did not settle until early July when large numbers reappeared and reached a density of 100–800 individuals per 100 cm² within a month, and a peak slightly higher

than this in late August and September. In contrast to the events of 1957 the settlement of *L. kefersteinii* in 1958 was more conspicuous, and the growth of individuals more rapid and vigorous, but this may have been due to lack of competition from other species, such as *B. amphitrite* and *D. listerianum*, which settled in smaller numbers during 1958.

L. antedonis has been recorded on the panels from January to July 1958, with maximum numbers of 100–200 individuals per 100 cm² settling in May and early June : thus only in July did the two species occur side by side.

Although the water temperature in the dock is at all times higher than that of the sea outside there are seasonal changes with a winter minimum in February and a summer maximum in July. The two species of *Loxosomella* show seasonal differences in the time of settlement, *L. antedonis*, the northern species, flourishes during the cooler months whilst *L. kefersteinii*, the southern form, is most conspicuous during late summer and autumn. Consequently, it would seem that the cessation of breeding of *L. kefersteinii* during the early months of the year is a result of lower temperatures rather than lack of food. The water temperatures in the dock accord well with those prevailing in the Adriatic (World Atlas of Sea Surface Temperatures, 1944), which represents the northern sector of *L. kerfersteinii*'s geographical range. Its reproductive season in the Adriatic is not, however, known. The only recorded locality for *L. antedonis* is off the north-east coast of Greenland on *Poliometra prolixa*, and it seems significant that the breeding season at Swansea coincides with the lower water temperatures. These are still considerably higher than the summer temperatures expected at a latitude of 77°N, for Koehler (1927) states that the temperature range of *Poliometra* is from —1°C to +1°C. However, it should be noted that some animal species can occupy an enormous geographical area : *Actinia equina* L., for example, has a range extending from the Arctic to the tropics (Stephenson, 1935). It is, therefore, possible that *L. antedonis* may extend over a considerable range, but has been overlooked on account of its small size.

THE FORMATION, RELEASE AND BEHAVIOUR OF BUDS OF *L. KEFERSTEINII* AND *L. ANTEDONIS*

During July, when both species of *Loxosomella* were settling simultaneously, it was possible to compare the development, release and subsequent behaviour of the buds. Individials of both species normally become sufficiently mature to produce buds in two weeks, although buds may begin to form on quite small animals. Fully grown buds, when ready for detachment from the parent, are relatively large and the lophophore is well developed. Such large buds become very active and exhibit convulsive twisting and writhing movements very like the avoidance reaction of the adult. These ultimately result in the breakage of the now slender union between the parent and the bud. It appears that when an adult bearing a large ripe bud is detached from the substratum and "handled" the bud breaks free more rapidly than if left undisturbed, but an exactly similar process of detachment has been observed in undisturbed groups of individuals. In a specimen of *L. kefersteinii* the detachment process was observed to last for about an hour. Throughout this time the adult

remained with its lophophore tightly closed, swaying gently from time to time. This behaviour was punctuated by a few vigorous " avoidance " movements of the peduncle which resulted in the calyx bearing the bud being swept against the substratum and surrounding objects.

Newly detached buds may behave in a number of ways. Commonly, in both species, the buds, still twisting and writhing, fall away from the parent, but almost immediately they swim off, usually upwards away from the panel often reaching the surface of the water above. The daughter zoids swim smoothly and rapidly with the lophophore expanded in front and the foot trailing. The actively beating cilia no doubt provide the propulsive power and also cause the animal to rotate in a torpedo-like manner. The swimming phase appears quite characteristic, and does not appear to have been previously recorded in the Loxosomatidae.

Either without swimming, or preceding or following it, a bud of *L. kefersteinii* may settle on a substratum and temporarily attach itself by its tentacles while the peduncle writhes and waves as though searching with its foot for a suitable surface. Alternatively it may attach by its foot and use the rest of the body to perform the waving and searching movements. By an extension of this behaviour it may even move over the substratum for short distances by a motion reminiscent of that of a looper caterpillar—a less pronounced, but basically similar process as has been observed in adults of *Loxosoma saltans* Assheton (1912). This behaviour in contact with a solid surface has not been observed in recently liberated buds of *L. antedonis*. After temporary attachment to a glass slide, however, a bud of the latter species has been observed to glide over the surface on the " sole " of its foot.

Since sexual reproduction has not been observed in either species, propagation appears to be principally by budding. It is probably the power of locomotion of the buds, both through the water and over the substratum that enables these two species to colonize recently immersed test surfaces so rapidly. This ability, together with rapid growth and early maturity, is clearly of importance for the survival of sub-microscopic organisms which are ousted by the larger forms becoming dominant in the later stages of ecological succession.

LOXOSOMA ANNELIDICOLA (Van Beneden & Hesse), 1864

This species was dredged from 18 m. at Holyhead, North Wales, in November 1957. It has a very characteristic flattened appearance and has aptly been likened to an elm samara (Prenant & Bobin, 1956, p. 34). The Holyhead specimen was 300 μ high and had thirteen tentacles. In drawings made by Prouho (1891) in an anatomical study on this species the lophophore appears to be terminal in position, whereas in the Holyhead specimen the characteristic lateral wings clearly continue around the distal side of the lophophore (Fig. 3).

L. annelidicola has previously been found associated with two species of maldanid polychaete : *Nicomache lumbricalis* (Fabr.) and *Petaloproctus terricola* Quatref. The present specimen was found on what was clearly the inner lining of a fragment of worm tube. Unfortunately, although all other

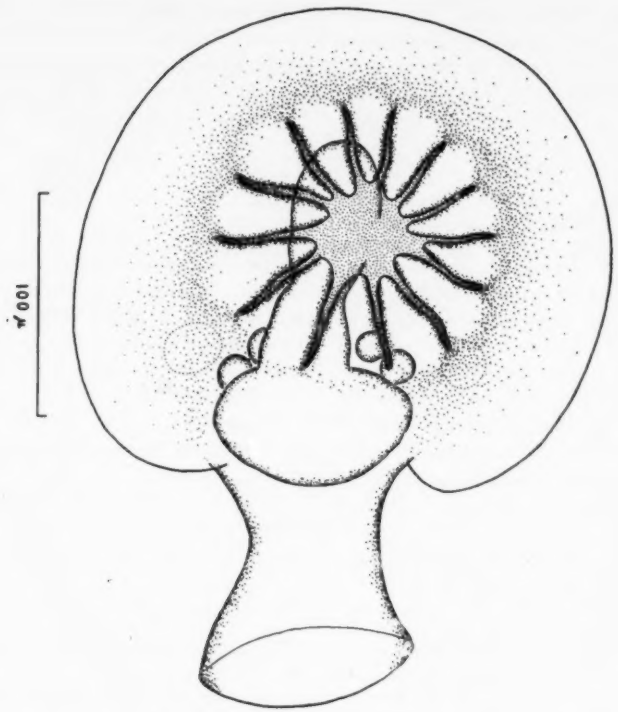

Fig. 3.—*Loxosoma annelidicola*. Oral view of specimen with tentacles withdrawn.

worms and tubes obtained from the locality were examined no further specimens of *Loxosoma* were found.

The species is small and easily overlooked and there seems no reason to regard it as a recent introduction. Both of its previous records come from the French coast of the English Channel.

SUMMARY

Three species of Loxosomatidae are reported from Britain for the first time. *Loxosoma annelidicola*, previously known from the Channel coast of France, has been dredged off the Anglesey coast. Two species of the normally epizoic genus *Loxosomella* have been found abundantly on test surfaces immersed in the warm dock at Swansea. One, *L. kefersteinii*, is a native of the Red Sea and eastern Mediterranean, and has evidently been carried to Swansea by ships passing through its native area ; the record is the first from western Europe. The second species appears quite indistinguishable from *L. antedonis*, a northern form never previously recorded from Europe. This species is fully described. It is pointed out that in Swansea docks the settlement of *L. antedonis* takes place early in the year and that of *L. kefersteinii* in the

late summer and autumn. The ability of the newly liberated buds to disperse, both by swimming and by progression over a solid surface is described, and the rapid colonization of immersed test surfaces so advantageous to such small organisms is presumably facilitated by these powers of locomotion. Specimens of both species of *Loxosomella* have been deposited in the British Museum (Natural History).

ACKNOWLEDGMENTS

We should like to express our gratitude to Mlle G. Bobin for confirming our identification of *L. kefersteinii* ; to Dr Daphne Atkins for examining and commenting on our specimens of *L. antedonis* ; to Professor E. W. Knight-Jones of the University College of Swansea and Mr O. Simmonite for undertaking the collection and dispatch of the settlement panels ; and to Mr. L. S. Thornes of the B.P. Refinery (Llandarcy) Ltd. for supplying temperature data. Our thanks are also due to Dr D. J. Crisp and Dr C. Burdon-Jones for their interest and assistance during the preparation of the manuscript and figures, and to the Development Commision and the Department of Scientific and Industrial Research for financial support.

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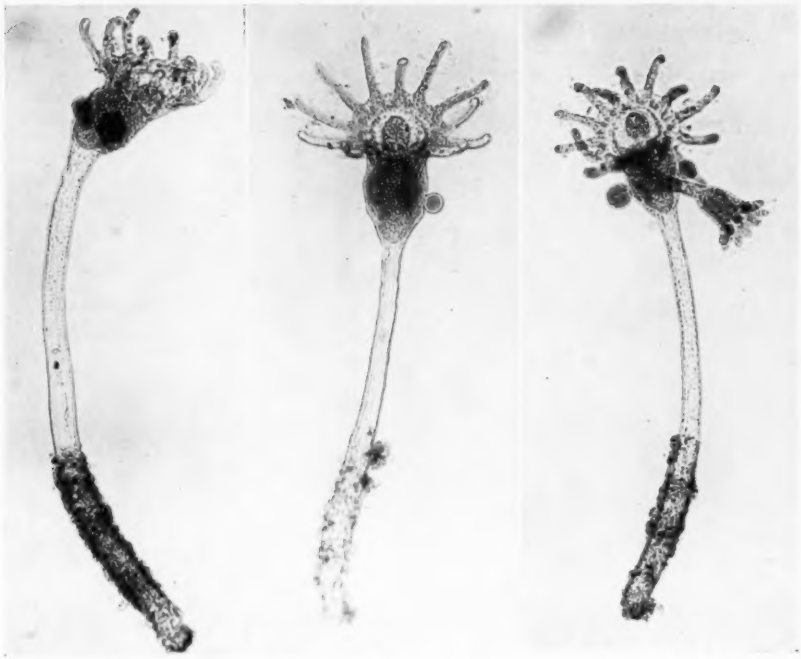

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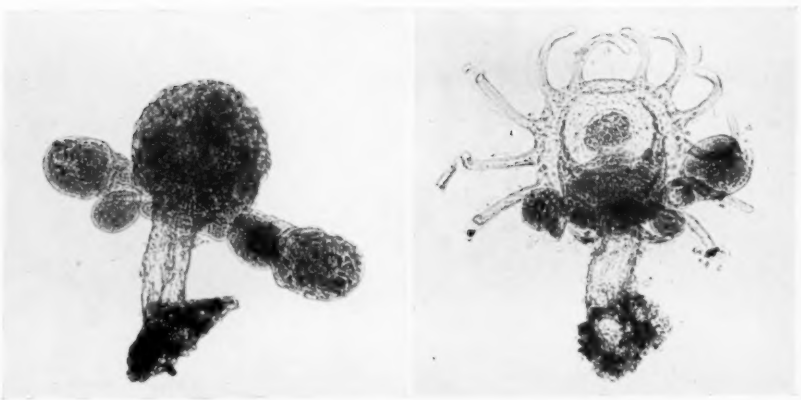

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1.—Photomicrographs of *Loxosomella kefersteinii*.
2.—Photomicrographs of *Loxosomella antedonis*.

EXPLANATION OF PLATE

Fig. 1.—Photomicrographs of *Loxosomella kefersteinii*. (a) Side view of specimen with two young buds. (b) Frontal view of specimen with one small bud. (c) Frontal view of specimen with two young buds and one large bud about ready for liberation. The long, free peduncle of the latter crosses the calyx and the foot is situated above the bud on the animal's right side. The appearance of the peduncle shown in all the specimens is very characteristic of *L. kefersteinii*, and the accumulation of debris around the lower region is typical of specimens from Swansea.

,, 2.—Photomicrographs of *Loxosomella antedonis*. (a) A frontal view of individual with closed lophophore, showing the typical appearance of a specimen about two weeks old. Four buds are present, and the manner in which budding takes place on alternate sides is clearly apparent from the size of the buds. There is no pedal disc, but a characteristic accumulation of debris surrounding the base of the peduncle. (b) Fully expanded (narcotized) individual seen from the front. The peduncle is somewhat curved and the foot shows clearly through the associated debris.

THE DEVELOPMENT OF THE PLEOPODS IN THE YOUNG CRAB STAGES OF *PINNOTHERES* (CRUSTACEA)

BY

D. ATKINS, D.Sc.

From the Marine Biological Laboratory, Plymouth

[Accepted 10th February 1959]

(With 13 figures in the text)

CONTENTS

	Page
Introduction	435
Development of the pleopods in *Pinnotheres pinnotheres* (L.) ..	436
The female	438
The male	442
Development of the pleopods in *Pinnotheres pisum* (Pennant) ..	446
The female	446
The male	447
Summary	451
References	451

INTRODUCTION

The results recorded in this paper are a small part of work on *Pinnotheres* carried out at the Plymouth laboratory from October 1927 to August 1929 and then from June 1952 to 1953, and including the rearing of tiny immature crabs in *Mytilus*.

In the megalopa of *Pinnotheres pinnotheres* and *P. pisum* the pleopods are of the usual type found in that post larval stage. There are four pairs only, on the second to fifth abdominal segments, and all are biramous, the exopodites being large and the endopodites small. The numbers of swimming setae and of hooks are not entirely constant (see Atkins, 1955, pp. 699, 705). The pleopods of a megalopa of *P. pinnotheres* are shown in Fig. 1, the swimming setae at full length on one pleopod only.

Unfortunately the first crab stage was not reared from the megalopa of either species, but some crabs taken from their hosts were tiny, being probably the second or third young crab stages. It is most probable that, contrary to the belief of Christensen (1958), the first crab stage of *P. pisum* will be found in *Mytilus*, at least in certain localities. My failure to find crabs of less than 1·4 mm. carapace width was almost certainly due to having to open and examine unaided bags of a thousand mussels only 8 to 25 per cent infected. Not having the time to examine the bivalves under a dissecting microscope, I relied on unaided sight. The mussels were obtained from firms supplying them for human consumption, and so the bags contained few small ones. This may well have contributed to my failure to find the first young crab stages, if these occur chiefly in the spat and young of their bivalve hosts, as do those of *P. ostreum* (see Christensen & McDermott, 1958).

An examination of the pleopods shows that in these two species of *Pinnotheres* the development follows that described by Cano (1892, see Gurney, 1942, p. 155) and Shen (1935) for *Carcinus maenas* ; the pleopods do not disappear and a second series arise as described by Hyman (1920) for *Gelasimus*. In *Pinnotheres* the female has only pleopods 2 to 5.

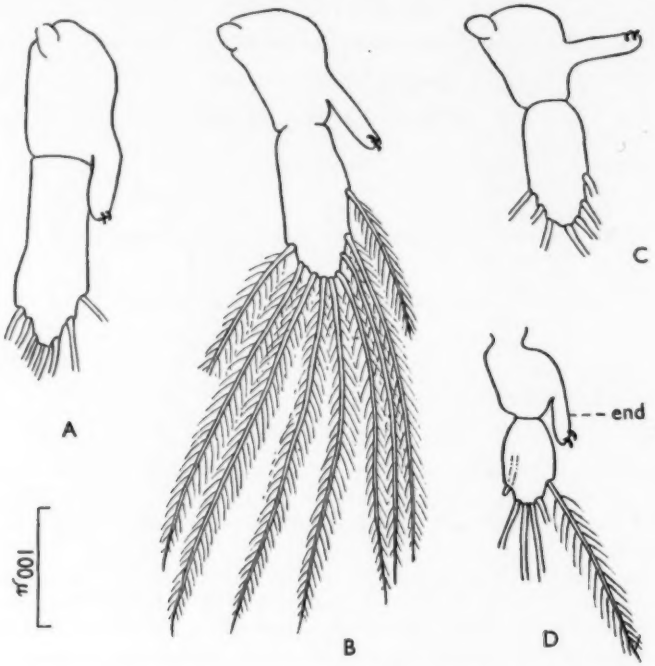

Fig. 1.—*Pinnotheres pinnotheres*, megalopa. A–D, pleopods 2 to 5. *end.*, endopodite.

DEVELOPMENT OF THE PLEOPODS IN *Pinnotheres pinnotheres* (L.).

In *P. pinnotheres*, in which there is no sexual dimorphism comparable to that in *P. pisum*, only one form of the male has been found (Atkins, 1958), and no sudden change in appearance of the female occurs during growth.

The megalopa of *P. pinnotheres* has a carapace width of 0·74 to 0·8 mm., and carapace length of 0·9 to 1·0 mm. (Lebour, 1928, p. 538 ; Atkins, 1955, p. 703), while the smallest crab, a female, taken from its host had a carapace width of 1·5 mm. The increase of 0·7 mm. in width may make it possible for this to be a second young crab stage, as from a carapace width of 1·5 mm. the increase between the next two or three moults was about 0·3 mm.

In *P. taylori*, Hart (1935, pp. 422–423) recorded an increase in width of about 0·2 mm. from the megalopa of 0·5 mm. carapace width to the first young crab stage, while in *P. ostreum* Sandoz & Hopkins (1947) found the increase

in width from a megalopa of 0·58 mm. to be only 0·01 mm. These were laboratory-reared crabs and therefore unlikely to increase in size as rapidly as crabs in the wild. Moreover, both megalopae were smaller than those of *P. pinnotheres* and the increase likely to be less than that from the large megalopa of the latter species. Christensen & McDermott (1958, p. 163) gave only one record of the moult of a first crab of *P. ostreum* into a second, with the small increase of 0·10 mm.

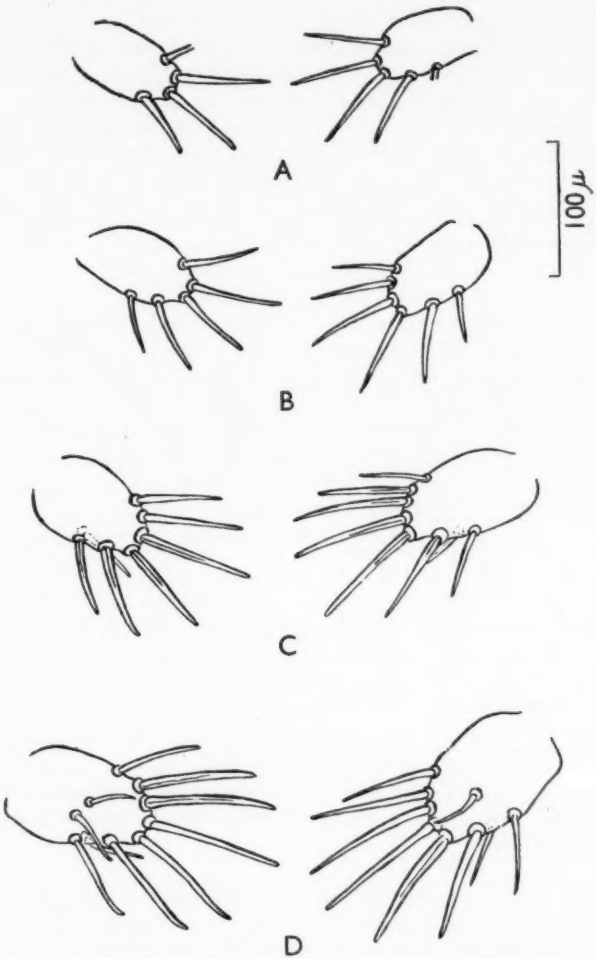

Fig. 2.—*Pinnotheres pinnotheres*, female. Dactyli of second maxillipedes, to illustrate increase in number of spines with age, from four successive cast integuments (A–D) of the same crab. Carapace width 1·56, about 2·0, 2·14 and 2·60 mm. respectively.

The number of spines on the dactyli of the second pair of maxillipedes (see Fig. 2) and the number of short curved setae in a small group posterior to the anus help to determine the stage of young crabs. In the only megalopa of which the maxillipedes were examined the dactyli of the second maxillipedes bore four spines : one anal seta was present.

The female

Second (?) *crab stage.* (Fig. 3 A and B 1)

Two crabs were found which might be considered to be this stage. Crab ' A ' : carapace width 1·5 mm. Four spines were present on the dactyli of the second maxillipedes : three or four anal setae were present.

In the megalopa the four pairs of pleopods were respectively 0·26, 0·23, 0·19 and 0·135 mm. long, while in this crab they were approximately 0·23, 0·19, 0·14 and 0·09 mm. long. The exopodites were still large and the endopodites small ; setae were entirely absent from the pleopods (Fig. 3 A). Vaginae were present.

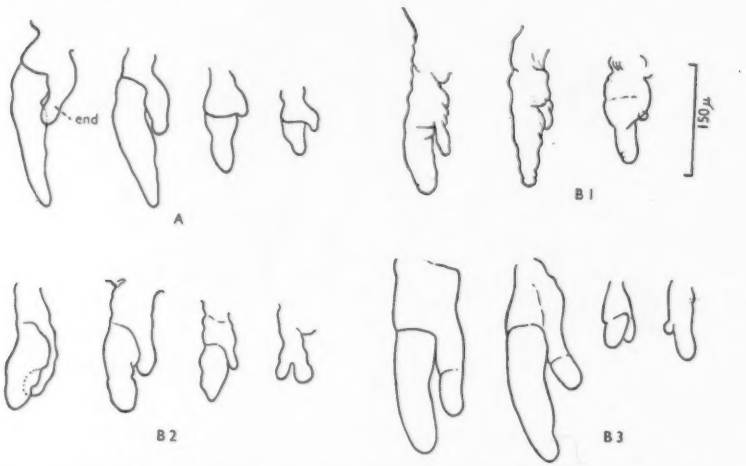

Fig. 3.—*Pinnotheres pinnotheres*, pleopods (2–5) of immature females. A. carapace width 1·5 mm.: B, 1–3 successive stages of one crab, carapace width 1·52, 1·92 and 2,18 mm., the first two being cast integuments. Pleopod 5 of crab B 1 is not shown.

In this and the following figures of the female, pleopod 2 is on the left : the endopodite of each pleopod is on the right.

Crab ' B 1 '. The pleopods of the cast integument of a female of carapace width 1·52 mm. are also figured (Fig. 3 B1) as it moulted twice. Although slightly larger than the crab already described, it is possibly slightly younger, judging by the number of three spines on the dactyli of the second maxillipedes, the three anal setae and the absence of vaginae. The chitin of the pleopods in the cast skin was excessively thin and somewhat crumpled, but they had

much the appearance of those of crab ' A '. The last pair of pleopods were torn and could not be drawn.

The abdomen of the megalopa is about 0·82 mm. long and 0·26 mm. wide, while that of this crab is 1·08 long and 0·58 mm. wide.

Third (?) *crab stage.* (Fig. 3 B 2).

Crab ' B 2 '. The next stage of this crab had a carapace width of 1·92 mm. (cast skin), an increase of 0·4 mm. Four spines were present on the dactyli of the second maxillipedes : the number of anal setae was four : vaginae were still not discernible. The endopodites had increased in length, and the exopodites of pleopods 4 and 5 decreased in length.

Fourth (?) *crab stage.* (Fig. 3 B 3).

Crab ' B 3 '. The following stage had a carapace width of 2·18 mm., an increase of 0·26 mm.: unfortunately the crab died in this stage. Five and six spines were present on the dactyli of the second maxillipedes ; anal setae could not be counted. Vaginae were now present. Pleopods 2 and 3 had increased in size : the endopodites were much longer than in the previous stage and showed a distinct suture, but were still shorter than the exopodites. The exopodites of pleopods 4 had decreased in length and the endopodites increased, so that they were now of about equal length. The endopodites of pleopods 5 had increased in length, while the exopodites were minute.

Crab ' C 1 '. A crab of carapace width 2·14 mm. moulted twice. Although slightly smaller than crab ' B 3 ' it was probably at about the same stage, pleopods 4 and 5 were larger, but their exopodites smaller. Pleopods 2 and 3 could not be got into a good position for examination, however, the endopodites and exopodites appeared to be about the same length. This crab had seven and eight spines on the dactyli of the second maxillipedes.

Fifth (?) *crab stage.* (Fig. 4 A).

Crab ' C 2 '. In the next stage of crab ' C ' the carapace width was now 2·60 mm. (cast skin), an increase of 0·46 mm. Nine and ten spines were present on the dactyli of the second maxillipedes; the number of anal setae was seven. The pleopods had again increased in size. The endopodites of pleopods 2 were considerably longer than the exopodites. Pleopods 3 were both unfortunately crumpled and useless for measurements. Pleopods 4 and 5 were uniramous, as in the adult, but a small protuberance near the base was probably a rudiment of the exopodite. The endopodites of all pleopods had each a single suture.

Sixth (?) *crab stage.* (Fig. 4 B).

Crab ' C 3 '. This stage had a carapace width of 3·39 mm., an increase of 0·79 mm.: the crab died without moulting again. The endopodites of pleopods 2 were much longer than the exopodites, as in the adult, and in pleopods 3 only slightly longer. The exopodites of pleopods 2 and 3 had two setae each.

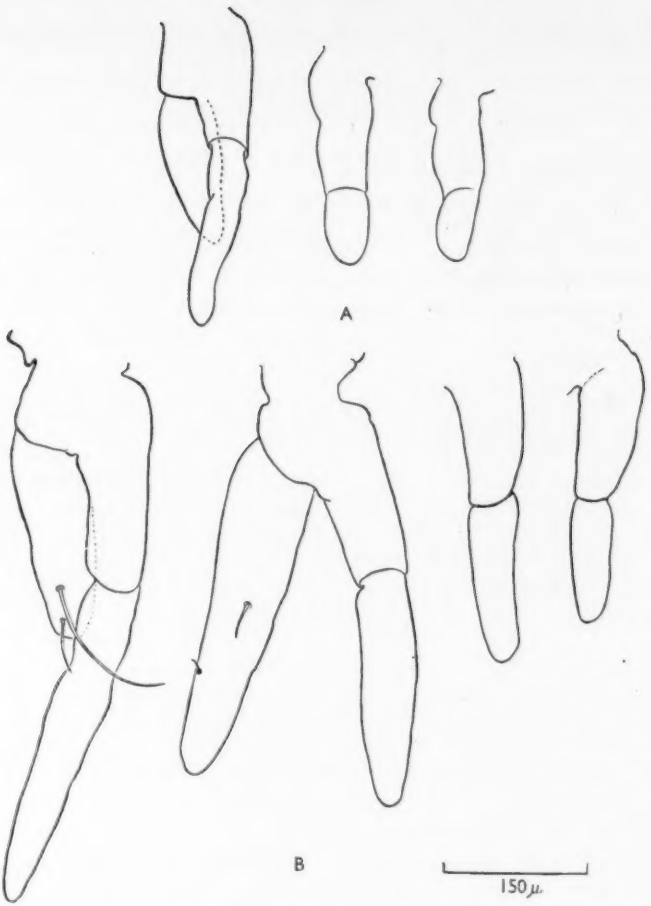

Fig. 4.—*Pinnotheres pinnotheres*. Pleopods from successive stages of one female ; carapace width A. 2,60 mm. (cast skin) and B. 3,39 mm. (crab). Both pleopods 3 of the cast were too crumpled to be drawn.

Seventh (?) *crab stage.* (Fig. 5).

At a carapace width of 3·9 mm., and with abdomen still narrow and resembling that of the male in shape, the pleopods were larger and more setose than in the previous stage, but there was little difference in the proportion of the endopodite to exopodite of pleopods 2 and 3. A crab with narrow male-like abdomen, and carapace width 4·9 mm. had the pleopods little more advanced than in that 3·9 mm. wide.

Further stages will not be given, but it may be mentioned that at a carapace width of 5·65 mm. the abdomen had widened and was in the second stage of

development. The endopodites of pleopods 2 were longer in relation to the exopodites than at a carapace width of 3·9 mm. The endopodites of pleopods 3 were still only slightly longer than the exopodites. All pleopods were more setose.

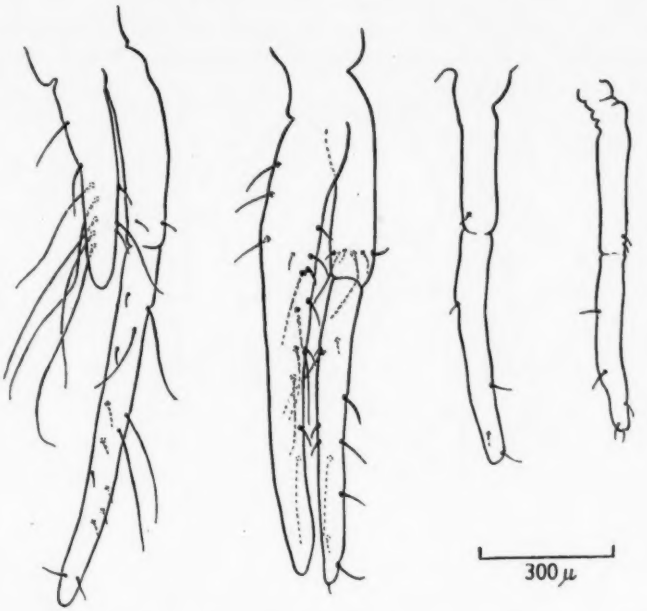

Fig. 5.—*Pinnotheres pinnotheres*. Pleopods of female of carapace width 3·9 mm. Side hairs omitted from the setae.

Some variation occurs in the development of the pleopods in crabs of approximately the same carapace width, but growth of pleopods 2 consists in lengthening of the endopodite in relation to the exopodite : the endopodites and exopodites of pleopods 3 remain at about the same relative length, until at a carapace width of 3·4 to 3·9 mm. the endopodites are slightly the longer, and not more so at a carapace width of 4·9 mm. The growth of pleopods 4 and 5 consists of lengthening of the endopodites and reduction and final disappearance of the exopodites, but here again there is some variation.

In the very young stages setae are absent from the pleopods ; at a carapace width of 3·39 mm. two are present on the exopodites of pleopods 2 and 3 ; none on pleopods 4 and 5. At a carapace width of 3·9 and 4·9 mm., with narrow abdomen, setae are present on all pleopods. At a carapace width of 5·6 mm., with the abdomen in stage II, setae had increased in numbers : in the following stages, as the abdomen widens, the pleopods become yet more hairy. The pleopods of the adult female *P. pinnotheres* resemble those of the adult *P. pisum* in hairiness (see Atkins, 1926, pl. 5, figs. 29, 30).

The male

The smallest male *P. pinnotheres* collected had a carapace width of 1·96mm.: this would probably correspond with what has been designated the third (?) young crab stage of the female. The female of this stage had four spines on the dactyli of the second maxillipedes and so had this male. The number of these spines is evidently not entirely constant in crabs of about the same carapace width, for a male of 2·26 mm. width also had only four spines.

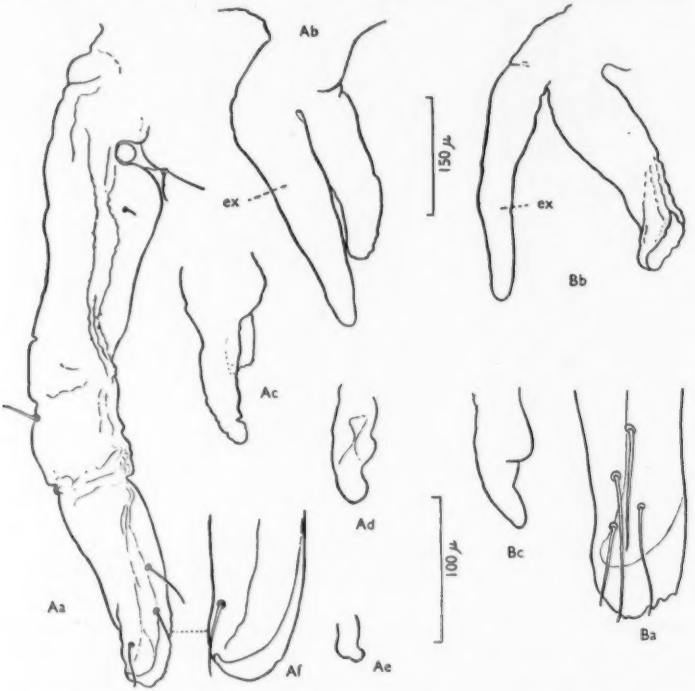

Fig. 6.—*Pinnotheres pinnotheres*. Pleopods from successive stages of one male, carapace width A. 2·26 mm. (cast skin) and B. 2·5 mm. (crab). Aa–Ae pleopods 1–5 ; Af. end of first enlarged. Ba. end of first pleopod ; Bb. second pleopod ; Bc. third pleopod. Pleopods 4 and 5 were uniramous and are not illustrated. Aa–Ae and Bb, Bc to upper scale : Af and Ba to lower scale. ex., exopodite.

In the male of carapace width 1·96 mm. the pleopods on the first abdominal segment—not represented in the megalopa—were already well formed, about 0.81 mm. long, reaching to the mid-region of the fifth abdominal segment : each had a rounded tip and bore two or three setae. The second pair were biramous, the exopodites longer than the endopodites. Pleopods were also present on the third to fifth segments, but were small, decreasing in size posteriorly ; all but those on the third were uniramous, the endopodites having

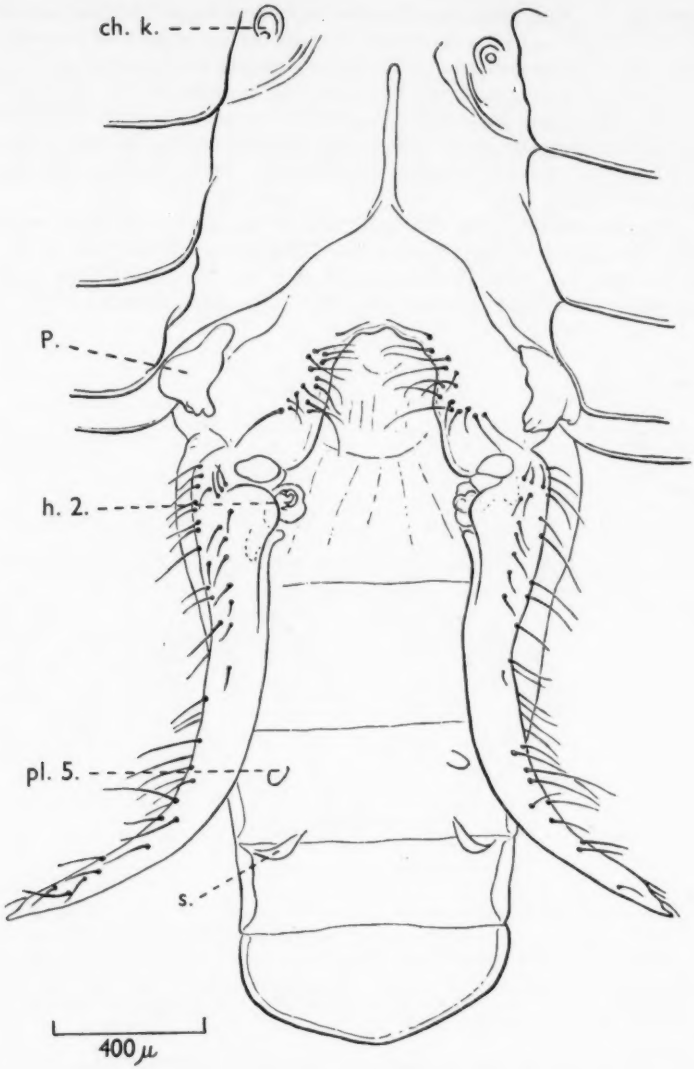

Fig. 7.—*Pinnotheres pinnotheres*. Abdomen with pleopods (cast integument) of male of carapace width 3·2 mm. Owing to the extension of the abdomen the head of the second copulatory appendage (h.2) has been pulled from the groove of the first ; the appendage is nearly upright. The last few segments of the abdomen are curved ventrally and therefore it does not appear at its full length. ch.k., chitinous knob and s., socket of locking apparatus of the abdomen. P., male papilla ; pl. 5, pleopod 5.

disappeared. Male papillae were present, but owing to the poor condition of the crab, which had been dead some time before being put in a preservative, it is impossible to discern whether the canals opened to the exterior.

In a crab of carapace width 2·26 mm., and possibly in the fourth young crab stage, there was little change. Pleopods 1 and 2 were slightly more advanced, but pleopods 3 to 5 not as degenerate as in the smaller crab, only the last being minute and uniramous (Fig. 6 A). Male papillae, with distinct ducts, were present.

In the post moult from this crab, which now had a carapace width o 2·5 mm., the copulatory appendages were further developed (Fig. 6 B) ; the tip of the first had three serrations, but it is not known whether these are always present in crabs of about this size. The inner ramus of the second

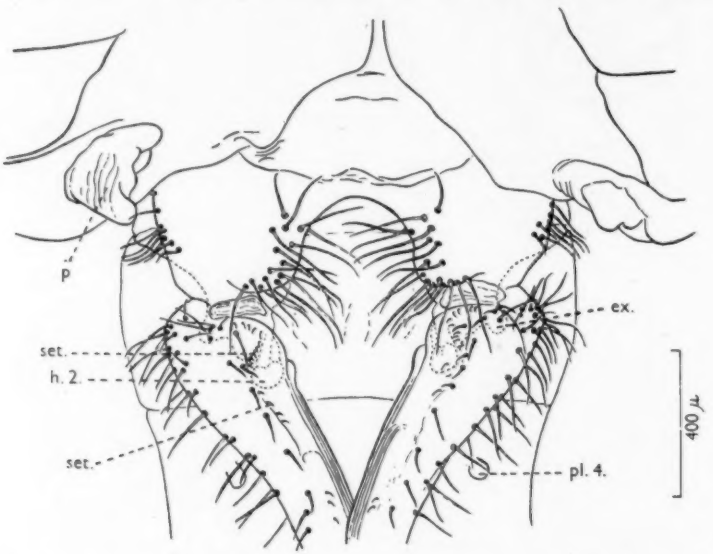

Fig. 8.—*Pinnotheres pinnotheres*. Proximal region of the abdomen of male of carapace width 3.5 mm. enlarged. (The next cast of the male shown in Fig. 7). Although the abdomen was held open by a cover slip, the heads of the second copulatory appendages (h.2) are still within the grooves of the first, on the inner walls of which are minute curved setae (set.). ex., exopodite of the second appendage shown by broken lines ; p., male papilla. Abdominal hairs omitted.

showed the beginning of the characteristic head of this appendage : the exopodite was still slightly the longer of the two. Of pleopods 3 to 5, the endopodites of the third were still visible, the fourth and fifth were uniramous and are not illustrated.

The first copulatory appendages. In males of increasing carapace width the first pair of copulatory appendages gradually increase in length, finally reaching as far posteriorly as the mid region of the telson. They also gradually become

more setose and the tip of each is produced into a spinous projection (Fig. 7). The degree of hairiness varies in crabs of about the same carapace width, one of 2·26 mm. had some eight setae, while one of 2·14 mm. had seventeen on one surface alone. Minute curved setae with tips directed distally are present in the groove or canal (Fig. 8). Rosette glands occur in the thick part of the appendage, extending as far distally as the position reached by the head

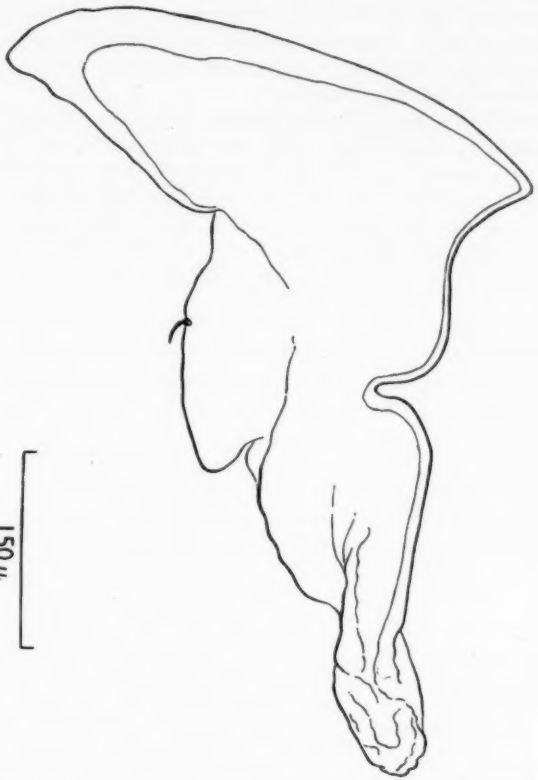

Fig. 9.—*Pinnotheres pinnotheres* : male of carapace width 4,0 mm. Second copulatory appendage still bearing an exopodite : drawn from crab.

of the second. The bases of the first pair meet in a ridge across the first abdominal segment (Figs. 7, 8). The appendages differ in the adult from those of *P. pisum* in having spinous projections and a rounded lobe near the apex, on the surface facing the abdomen.

The second copulatory appendages. Some variation occurs in the development of these appendages in males of about the same carapace width. The endopodite gradually increases in length and develops the characteristic

head. The exopodite gradually becomes smaller, but is present in males of a carapace width of at least 7·0 mm., that is near the largest size found. The second copulatory appendage of a male of width 4·0 mm. is shown in Fig. 9.

The third to fifth pleopods. These are still present in the male of carapace width 4·0 mm., although the last pair are minute. Unfortunately no males were obtained of a carapace width of between 4·0 and 6·3 mm.; at the latter size the first to the fourth pairs were present, although the last two pairs were minute. This crab died in moulting, however it could be seen that four pairs would again be present in the post moult. At a carapace width of 7·0 mm. only the two pairs of copulatory appendages were present ; the second still with an outer, although tiny, ramus.

Compared with the male *Carcinus maenas*, pleopods 3 to 5 of the megalopa persist, although in rudimentary state, through more stages of the male *P. pinnotheres*, and are still present when the copulatory appendages are fully developed and functional. In *Carcinus maenas* the third, fourth and fifth pairs have disappeared by the fourth young crab stage, although a vestige of the exopodite of the second pleopod persists to the fifth stage (Shen, 1935). It will be seen that they also persist longer in *Pinnotheres pinnotheres* than in *P. pisum*.

THE DEVELOPMENT OF THE PLEOPODS IN *Pinnotheres pisum* (PENNANT)

The megalopa of *P. pisum* has a carapace width of about 0·55 to 0·57 mm. and carapace length of 0·55 to 0·69 mm. (Atkins, 1955), while the smallest crab taken from its host was a male with carapace width 1·40 mm.; this must be far from being the first crab stage. Christensen (1958) has described the first crab stage of *P. pisum* taken from *Spisula solida* as having a carapace width of about 0·7 to 0·75 mm. It therefore does not seem worthwhile attempting to place the smallest crab obtained in a growth stage.

The female

The two smallest female *P. pisum* obtained had both a carapace width of 1·56 mm., were thick-shelled, with colour pattern and with swimming hairs on the legs: the abdomen was narrow and male-like. The development of pleopods 2 and 3 was at about the same stage as in the third (?) stage of *P. pinnotheres*, the exopodites being large and the endopodites short : pleopods 4 and 5 were more advanced showing no indication of being biramous (Fig. 10 A). Vaginae were present.

In a female of carapace width 1·91 mm. (thick-shelled, with colour pattern, with swimming hairs and male-like abdomen) pleopods 2 and 3 had both rami of approximately equal length : the endopodites consisted of two segments (Fig. 10 B). Pleopods 4 and 5 were uniramous, and longer than in the previous crab.

In a female of carapace width 2·34 mm., of the same appearance as the two previously described and also with male-like abdomen, the endopodites of pleopods 2 were longer than the exopodites, while the reverse occurred for pleopods 3. The endopodites of all pleopods had two segments. A few setae were present on pleopods 2 and 3 (Fig. 10 C). In the first two pairs of

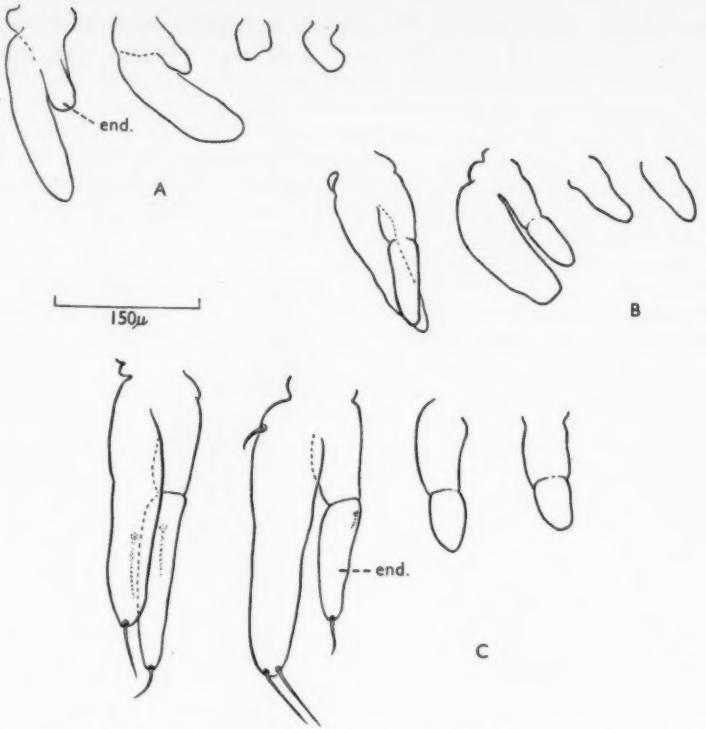

Fig. 10.—*Pinnotheres pisum*. Pleopods (2–5) from three females of the following carapace width : —A. 1·56 mm. ; B. 1·91 mm. ; C. 2·34 mm. All were thick shelled, with colour pattern, swimming hairs and narrow male-like abdomen. A and B drawn from crab ; C from cast integument with abdomen in position. end., endopodite.

pleopods the proportion of endopodite to exopodite was about the same as in the fifth (?) stage of *P. pinnotheres*, but at that stage the latter species had no setae on the pleopods.

At a carapace width of 3·5 mm., thick-shelled, with colour pattern, swimming hairs and narrow male-like abdomen, pleopods 2 had the endopodites nearly twice the length of the exopodites, while pleopods 3 had the two rami of about equal length. This, and further stages, in the development of the pleopods of the female are shown in Atkins, 1926, pl. v. It should be noted that in that paper the four pairs of pleopods were named first to fourth, and not according to the abdominal segment on which they occured.

The male

In *P. pisum*, in which there is striking sexual dimorphism, the male occurs under two main forms :—(a) thick-shelled, with conspicuous colour-pattern, provided with swimming hairs on certain of the legs : (b) thin-shelled, without pattern and without swimming hairs (Atkins, 1958).

The smallest male obtained of carapace width 1·40 mm. was of form (a) and was possibly the third or fourth young crab stage. It had three pairs of pleopods only, present on the first, second and third segments of the abdomen (Fig. 11 A) : those on the fourth and fifth segments had already disappeared. The first pleopod was of the same form as the copulatory appendage in the adult male, but reached only just within the posterior border of the sixth segment of the abdomen, whereas in the adult it reaches into the seventh and last segment. It also differed from the adult in that only two or three setae were present (Fig. 11 A).

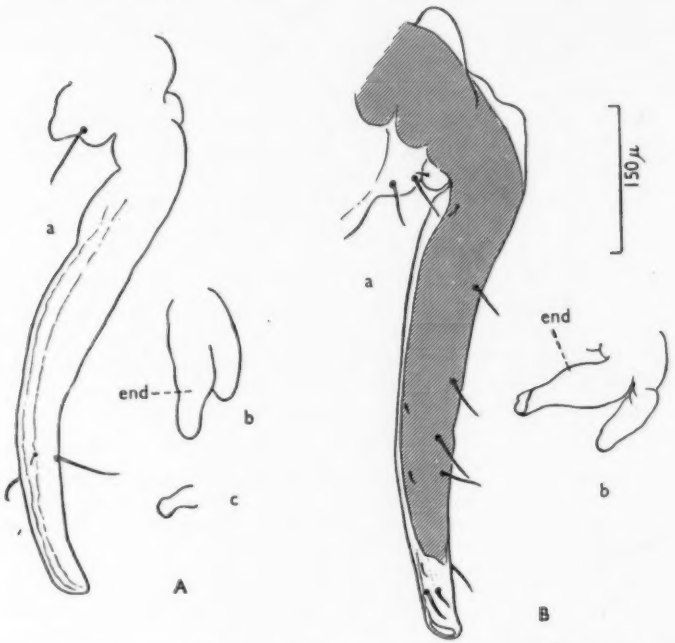

Fig. 11.—*Pinnotheres pisum*. Pleopods from two males of carapace width A. 1·40 mm. B. 1·44 mm. Both were thick-shelled, with colour pattern and swimming hairs. Aa–Ac, pleopods 1–3 ; pleopods 4 and 5 were wanting (drawn from crab). Ba and Bb, pleopods 1 and 2 ; pleopods 3–5 were wanting : the partly with-drawn first appendage of the post-moult is shown shaded. end., endopodite.

The second pleopods were biramous and without setae. The endopodite was longer than the exopodite : the endopodite had not the characteristic form of that of the adult, but it is probable that its tip was carried within the groove of the first appendage. In separating the abdomen from the thorax the second appendage is usually pulled from the groove of the first, but its normal position within the groove can be seen in cast integuments—especially clearly in thin ones—in which the abdomen remains locked to the thorax.

The third pair of pleopods were small, uniramous and without setae. Male papillae were present.

The post moult of this crab was badly contorted, it could, however, be seen that the endopodites of the second pleopods were now longer ; they were still without the characteristic head present in the adult. The testes were visible as narrow lobulated strands.

A slightly larger crab, carapace width 1·44 mm., also of form (a) had the first and second appendages more advanced in development than in the crab just described. The first appendages had a few additional setae and the endopodite of the second showed the beginning of the spoon-shaped head (Fig. 11 B). Pleopods 3, in addition to 4 and 5 were missing. The crab died in moulting, however, it was possible to see that in the post-moult the second appendage, although still biramous, had a distinct spoon-shaped head to the endopodite.

In a crab of carapace width 1·72 mm. of form (a) the two pairs of copulatory appendages alone were present. The first, which bore many setae, reached to the seventh segment of the abdomen, whilst the second pair had a definite spoon-shaped head to the endopodite. Fig. 12, drawn from a cast skin, shows

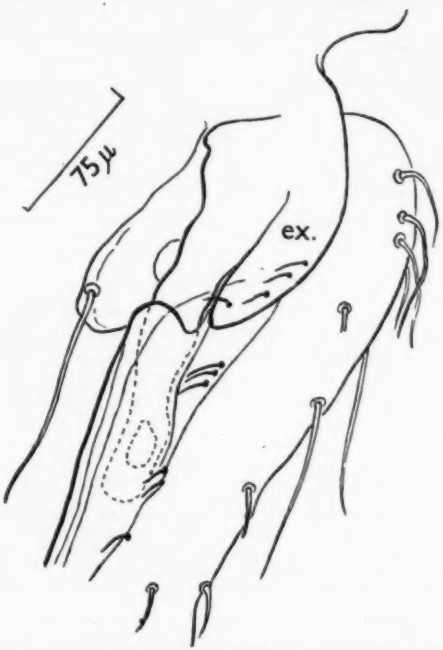

Fig. 12.—*Pinnotheres pisum* : male of carapace width 1·7 mm.; thick-shelled, with colour pattern and swimming hairs. To show the head of the second copulatory appendage (broken lines) within the groove of the first, but with the exopodite (ex.) outside the groove. The tiny, curved setae within the groove are shown solid. Drawn from cast integument, the abdomen locked to the thorax, and the appendages seen through the abdomen.

the head of the second appendage within the groove of the first, and also that the exopodite of this appendage does not enter the groove. Another male of carapace width 1·75 mm. had the appendages in about the same condition.

The first copulatory appendage of an adult male is figured in Atkins, 1926, Fig. 1.

The disappearance of the exopodites of the second appendages is variable (Fig. 13 A, B), and in males of about 3·0 mm. carapace width may be large on the appendage of both sides, large on one and absent on the other, or may be tiny on one or both. A crab which moulted three times is of interest in that the exopodite could be traced through four stages : it did not become smaller,

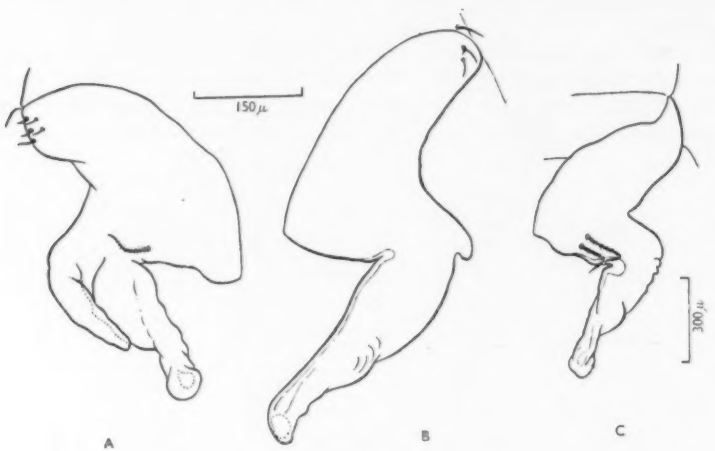

Fig. 13.—*Pinnotheres pisum*. Second copulatory appendages of the male, showing reduction in size and gradual disappearance of the exopodite. At carapace width of :—A. 2·9 mm. (the left appendage lacked an exopodite); B. 3·05 mm.; C. 5·3 mm. A and B were thin-shelled, colourless and lacked swimming hairs : C was thick-shelled, patterned and had swimming hairs.

but slightly larger in stages of carapace width 2·26, 3·04, 3·12 mm. and in the post-moult, which could not be measured as the crab died in moulting and the integument was pulled from it in pieces. It might be noted that Shen's (1935) figures 6 and 7 of the fourth and fifth young crab stages of *Carcinus maenas* show variation in reduction of the exopodites of the second appendages of the two sides.

The second copulatory appendage of an adult male of form (a), carapace width 5·3 mm., is shown in Fig. 13 C. The two long setae are not always found, and a few short ones may be present in other positions.

I am indebted to Dr I. Gordon for kindly reading the manuscript.

SUMMARY

The four pairs of pleopods of the megalopa persist in the females of *Pinnotheres pinnotheres* and *P. pisum*, undergoing modification to form the pleopods of the adult. The endopodites gradually become larger and the exopodites smaller, disappearing entirely from the last two pairs at about the fifth young crab stage. In the female *P. pinnotheres*, in which the series of growth stages obtained was fuller than in *P. pisum*, the pleopods were hairless to about the fifth crab stage : at the next stage a few setae had appeared, and these increased in numbers and length in the following stages.

The smallest male *P. pinnotheres* found, of carapace width 1·96 mm., had the first pair of pleopods—not represented in the megalopa—well formed. In addition, the four pleopods (2–5) of the megalopa persisted. Pleopods 2 and 3 were biramous, while 4 and 5 were tiny and uniramous, the exopodites having disappeared. In a crab of carapace width 2·5 mm. the inner rami of the second pair of pleopods showed the beginnings of the characteristic spoon-shaped heads present on the copulatory appendages of the adult. The exopodites gradually become smaller, but are recognisable in large males of carapace width of at least 7·0 mm. In a male of carapace width 4·0 mm. five pairs of pleopods were present, the last three being minute ; at a carapace width of 6·3 mm. two pairs of minute pleopods persisted in addition to the copulatory appendages, but at a carapace width of 7·0 mm. only the latter were present.

The smallest male *P. pisum* found, of carapace width 1·40 mm., had only pleopods 1 to 3, the last being minute and uniramous. At a carapace width of 1·44 mm. the two pairs of copulatory appendages alone were present. The second pair, still biramous, showed the characteristic spoon-shaped head on the endopodite at a carapace width of 1·7 mm.: the exopodite is variable in its disappearance, but would seem to be generally lacking in males of about 3·5 mm. carapace width.

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THE DEVELOPMENT OF THE WHISTLING FROG *ELEUTHERODACTYLUS MARTINICENSIS* OF BARBADOS

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CONTENTS

	Page
Introduction	453
Material and methods	454
Results	454
Gastrulation	455
Organogenesis	457
Discussion	466
Summary	467
Acknowledgments	467
References	468
Explanation of plates	468

INTRODUCTION

Eleutherodactylus martinicensis (formerly *Hylodes martinicensis*) is an inhabitant of Barbados, and other islands of the West Indies. Locally the animal has been named the " whistling frog " as a result of the persistent shrill piping noise which it emits during the evening. Altogether some 200 species of *Eleutherodactylus* are known to exist (Dunn, 1944), forming a large portion of the amphibian fauna of Central America and the West Indies. Since the introduction of the frog to Barbados, believed to be some time after 1850, it has spread all over the island establishing itself as a permanent resident, no doubt being aided by suitable environmental conditions. Its coloration, habits and breeding characteristics have been described by Bayley (1950).

The earlier literature on the development of *Eleutherodactylus* is tenuous and uninformative. Bavay (1873) in a one-page summary described the external appearance of the embryo during the fourth to tenth days. A further contribution by Peters (1876) compares *Eleutherodactylus* with other amphibia.

One of the most interesting features of the development of *Eleutherodactylus*, which takes place on land, entirely within the embryonic egg membranes, is the absence of a tadpole stage (Bavay, 1873 ; Lynn & Lutz, 1946) ; at the end of ten days, a miniature frog liberates itself by means of an egg tooth from the surrounding membranes. In accordance with the terrestrial mode

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of development, the egg membranes, whose prime function is protection, are tough and extremely thick. This resilient cover consists of an inner (vitelline) membrane investing the yolk surface, and an outer transparent membrane, between which are interposed successive layers of jelly. The vitelline membrane is firmly adherent to the surface of the egg (Bayley, 1950), but prior to the commencement of the formative movements of gastrulation it recedes towards the outer membrane.

Although the egg is medialecithal, cleavage is holoblastic and follows a similar pattern to that of a typical medialecithal egg (Sampson, 1904).

Lynn (1942) has thoroughly investigated the development of *E. nubicola*. Since the period of development in this species lasts 26 days and since, as the investigations of Sampson (1904) are claimed by Lynn to have been conducted on several species of *Eleutherodactylus*, it was decided to report the results of an investigation of the development of *E. martinicensis*. Only those aspects of the development of this species which have not been mentioned by, differ in particulars from, or expand the accounts of Sampson and Lynn will be described.

MATERIAL AND METHODS

Twenty eggs of *E. martinicensis*, representing nine different days of development up to the time of hatching, were examined histologically. The material was fixed in Heidenhain's Susa reagent, and wherever possible the protective egg membranes removed ; nevertheless the embryos were often extremely difficult to section histologically. After being blocked in paraffin wax, they were serially sectioned at a thickness of 5 μ, and stained by Ehrlich's haematoxylin and eosin. Most eggs were sectioned in the coronal plane, but owing to difficulty in orientation some were sectioned obliquely. For convenience in description each egg is referred to as a stage of development of the animal. Twenty-one eggs, stripped of their membranes were also investigated by high power binocular microscopy after clearing in Supracedrol.

RESULTS

Twenty-four hours after fertilization (stage I) the formative movements of gastrulation are well under way. The embryo is flattened dorso-ventrally, and possesses approximately a semi-circular outline in transverse section. The original blastocoele is already practically obliterated, and the gastrocoele is being formed. At this stage of late gastrulation, the roof of the gastrocoele is a flattened trilaminar plate composed of ectoderm, mesoderm and yolk endoderm from without inwards, whilst the floor and side walls are lined by yolk endoderm.

In stage II (48 hours) the general pattern of the embryo is well established. The blastocoele has been completely obliterated, and a reduction in the yolk endoderm has occurred. Growth has resulted in the expansion of the embryo cephalo-caudally and bilaterally over the surface of the reduced yolk mass. Cephalically a primitive head region is present, whose folding downwards on to the yolk mass has resulted in the formation of the primitive stomodaeum. Caudally the formation of a tail region similarly produces the proctodaeum.

The neural tube is closing (Pl. 1, fig. 2). Already distinction between an expanded brain region and a more elongated primitive spinal cord is evident. The notochord lies immediately subjacent to the neural tube. In the head region the primordia of the eyes form lateral diverticula of the future prosencephalon, whilst two localized bilaterally placed ectodermal thickenings indicate the areas of the olfactory and otic placodes. The lateral plate mesoderm has grown between ectoderm and yolk endoderm, and nearly approximated in the mid-ventral line. Dorsally this mesoderm has split to form the body cavity, in consequence of which the lumen of the gastrocoele has been considerably reduced. The primordia of the heart, liver, pancreas and pronephros are present. A rudimentary tail has been formed, whilst knob-like condensations of mesoderm indicate the site of the fore- and hind-limb buds. Finally, some eight or nine somites have been elaborated.

In stage III (72 hours) the chief structures laid down in the previous stage have been elaborated, and further growth has taken place, again at the expense of the yolk mass. The primitive divisions of the brain are evident (Pl. 1, figs. 5 and 6 ; Pl. 2, figs. 7 and 8), whilst the spinal ganglia are placed along the dorso-lateral aspect of the cord. The eye has expanded and bulges prominently from the antero-lateral aspect of the head, and now consists of an optic cup and lens. The pronephros has expanded and its duct has formed. Further growth and vascularization of the tail, in accordance with its respiratory functions, has occurred. Meanwhile the somites have differentiated.

During stage IV (96 hours) the pronephros starts to regress with the appearance of the mesonephric tubules. Nerve rootlets now connect the spinal ganglia to the cord. The primitive pre-cartilaginous blastemata of the skeletal system appear in the expanded limb buds. Finally the skin is now two layered, and pigment is being deposited in the inner layer.

From stage IV onwards, the embryo increases in size and complexity ; growth is rapid and the form of the animal is clearly approximating to that of the adult frog. Development from now until hatching is mainly concerned with the elaboration of the structures already established. The tail continues to expand up to stage VI, after which it undergoes regression, eventually forming the mere stump-like structure which is present at hatching. At stage VII (168 hours) a clump of ectodermal cells is present at the tip of the snout, which later becomes cornified and pigmented forming an egg tooth. Elaboration of all systems continues, until at the end of stage IX (216 hours) a miniature image of the adult frog is produced, whose size naturally can be no greater than that of the original egg.

Gastrulation

Stage I corresponds to one of late gastrulation, which follows the typical amphibian pattern. The original blastocoele has been reduced to a mere slit-like space, and the gastrocoele has become fully established. Cell differentiation and proliferation are well marked at this stage, and the three embryonic layers are easily recognized. The margins of the blastopore show signs of rapid proliferation and differentiation to form mesoderm, as a result of which the diameter of the blastopore has been reduced, prior to final closure by the

yolk plug. In consequence, the embryo as a whole has become reorientated within the egg membranes. The definitive dorsal and ventral surfaces are established, the blastopore is placed at the caudal end of the embryo, and the original animal pole has come to lie at the future cephalic end.

The gastrocoele shows variations in contour throughout its whole extent, yet its width remains relatively constant. Cephalically it presents as a mere slit-like space, which when traced caudally gradually expands, increasing in height, until it possesses a roughly semi-circular outline on transverse section in the mid region of the gastrula. From then on, as traced further caudally the lumen attains its greatest size prior to final reduction as the region of the blastopore is reached. The floor and walls of the gastrocoele throughout its whole extent are lined by yolk endoderm and show no special variations from region to region. The roof, however, shows several interesting features, and varies in constitution and thickness.

Cephalically the roof is a horizontal, thick and trilaminar plate, composed from without inwards of ectodermal, mesodermal and endodermal cell layers, the ectoderm forming a thick layer of neuro-ectodermal cells which are continuous bilaterally with the ectoderm covering the whole embryo. The mesodermal cell layer is likewise several cells in thickness, and is restricted to the middle third of the roof plate. The inner endodermal layer is continuous with the yolk endoderm ; it is also several cells in thickness.

The embryonic roof plate is grooved in the middle third of the mid-dorsal line to form the primitive groove. Further caudally this invagination is met by a corresponding evagination of the gastrocoele (Pl. 1, fig. 1). Ultimately as the invagination and evagination become more pronounced, a free communication occurs between the exterior and the cavity of the gastrocoele. This communication, the neurenteric canal, may serve to equalise pressure between the extra-embryonic fluid and that of the fluid in the gastrocoele ; it would seem, however, that the fluid pressure in the gastrocoele is greater than that in the former at this stage, since loose yolk endodermal cells are present in the canal and the exterior.

Immediately caudal to the neurenteric canal the roof plate is bilaminar, since the yolk endoderm is here limited to the walls of the gastrocoele. The neuro-ectoderm is confined to the region in front of the neurenteric canal, and the ectoderm of this zone is a thin unicellular sheet, the general surface ectoderm. The mesodermal constituent of the roof plate here is secondary mesoderm which has arisen from the lips of the blastopore. It forms a very thick undifferentiated cell layer, which in the middle third of the roof plate is condensed to give the typical appearance of a primitive streak. From the latter extensive proliferation is taking place bilaterally to produce the lateral plate mesoderm, which has already grown between the surface ectoderm and yolk endoderm at the sides of the embryo. Cephalic proliferation of " primitive streak " mesoderm on either side of the chorda mesoderm, between the neuro-ectoderm and yolk endoderm has also apparently commenced.

ORGANOGENESIS

The cardio-vascular system

Heart.

In stage II the primordium of the heart is seen as a simple endothelial tube surrounded by a mass of condensed mesoderm, which lies in the anterior part of the coelom suspended by a dorsal meso-cardium which has already undergone fenestration (Pl. 1, fig. 2).

In stage III with the expansion of the developing liver and the appearance of the septum transversum, the pericardial cavity becomes separated from the abdominal portion of the coelom. The heart tube is now bent into an S-shaped structure, and the primitive divisions are established. Caudally a free communication exists between the thin-walled sinus venosus, common cardinal veins and liver sinusoids. The sinus venosus (Pl. 2, fig. 7) drains into a more dorsally placed atrium, which in turn empties into a thick-walled ventricle. The atrio-ventricular canal is a narrow orifice, which has been constricted by the formation of subendocardial tissue. From the ventricle a short conus arteriosus (Pl. 1, fig. 5) passes ventrocranially and divides at the edge of the pericardial cavity into left and right carotid arches. The interior of the heart primordia is lined by flattened endothelial cells which are continuous with the endothelial lining of the arterial and venous systems.

In stage IV the mesoderm has differentiated to form the myocardium. Further thickening and twisting of the heart primordia is noted, and the lumen of the ventricle contains numerous finger-like processes projecting inwards from the myocardial wall. The pericardial cavity and the surface of the myocardium are lined by flattened serous cells of the pericardium.

In stage V the heart primordia have undergone further enlargement and localised thickening, and with flexion of the head the divisions have come to occupy their definitive adult positions. The ventricle lies caudally and empties into a now more elongated truncus which passes ventral to the atrial region. A raised ridge on the dorsal wall of the truncus indicates the developing septum. At the junction of atria and ventricle, the edges of the orifices are raised by reduplication of the endothelium, to form the primitive atrio-ventricular valve complex. The sinus venosus is triangular in outline, and free communication between it and the liver is now absent. The large thin-walled atrium has been divided into left and right chambers by the development of an inter-atrial septum.

By stage IX the adult heart structure is apparent. The septum of the truncus now forms the spiral valve, and the heart structure is typically amphibian.

Blood vessels

Arteries

In stage III, the short ventral truncus terminates by dividing into right and left carotid arches which pass dorsally and caudally before uniting just caudal to the pronephros to form the dorsal aorta. The latter extends practically to the end of the embryo before dividing into right and left branches which

pass to the respective developing hind limbs. From the inferior angle of the termination a large caudally directed median branch passes to the tail ; in addition there are several smaller lateral branches, the most conspicuous being the renal artery.

In stage IV the carotid and systemic arches are present and from the conus arteriosus near the origin of the systemic arch artery a large vessel, the pulmonocutaneous artery, takes origin.

By stage V large laterally directed branches, the subclavian arteries, are seen arising from the arches. In stage IX the adult arterial tree is apparent. With the recession of the pronephros, the renal vessels take a lower origin. Finally the median caudal branch to the tail has been much reduced in size, in accordance with the rapid degeneration of this organ.

Veins

The embryonic venous system falls naturally into two compartments, the vitelline and systemic circulations.

In stage II the yolk surface is studded with several small vessels, which by stage III have formed large tributaries of the vitelline veins (Pl. 1, fig. 6) and contain large nucleated blood corpuscles whose cytoplasm is seen to be loaded with yolk. The further development of the venous system agrees with the account of Sampson (1904).

The alimentary system and gut derivatives

Mouth

In stage II the stomodaeum is obvious ; by stage III it has expanded, and is now bounded above by the fronto-nasal process, bilaterally by the maxillary processes, and inferiorly by the mandibular processes (Pl. 1, fig. 5). The mesoderm of the maxillary and mandibular processes has condensed to form the primordia of the quadrate and Meckel's cartilage. Expansion and fusion of the processes has taken place in stage IV, and thus the stomodaeum becomes narrowed ; the pre-cartilaginous blastemata of Meckel's cartilage have fused in the midline (Pl. 2, fig. 9) and become further differentiated. Meanwhile the original flattened ectodermal lining has differentiated to form cells with a more cubical shape. In stage V bilateral expansion of the stomodaeum is noted, and the bucco-pharyngeal membrane is no longer present. By stage IX the jaw margins and mouth cavity are lined by a stratified epithelium.

Pharynx

The primitive pharynx is seen in stage II as a slit-like cavity lined by yolk endoderm and separated from the stomodaeum by the buccopharyngeal membrane. In stage III the pharynx is established (Pl. 2, fig. 7) and pharyngeal pouches are present ; corresponding ectodermal grooves have formed. By stage IV the pharyngeal floor has endodermal pharyngeal grooves, and a well marked tuberculum impar is present. In stage V the endoderm of the pharynx has differentiated to form a flattened unicellular epithelial lining which is continuous with that of the primitive mouth cavity. None of the pouches can be demonstrated to open to the exterior, and no traces of internal

gill development are evident. By stage IX the adult pharynx is established, and the lining has become a stratified squamous epithelium. At the postero-superior angles of the pharynx, two large masses of mucous glandular tissue are developing.

Tongue

The primordium of the tongue is seen in stage IV (Pl. 2, fig. 9) projecting in an anterior direction into the pharyngeal cavity, attached to the floor of the pharynx in the mid-line in the region of the second pharyngeal arch. In stage VI it forms a conspicuous elevated body which is attached anteriorly to the internal aspect of the expanded mandibular processes. This is a very interesting developmental change when compared with the previous stage ; the explanation is presumably that the mandibular regions have contributed the greatest portion of the tongue and since the growth in this region exceeds that of the tuberculum impar, the whole structure has become reorientated in the mouth cavity. Hence the base has now shifted to the anterior region of the mouth floor, leaving the portion derived from the tuberculum impar as the " free " tongue tip.

A powerful retractor muscle, attached to the anterior jaw margin, has developed in stage IX, and forms the chief component of the extrinsic musculature (Pl. 3, fig. 11). The original cubical cell layer has differentiated to form a layer of small spheroidal cells. This is present over the dorsal and ventral free surfaces, but over the dorsum of the tongue base it forms a much thicker layer. The epithelium lies on a well marked basement membrane separated from the underlying intrinsic musculature by a thin layer of fine connective tissue. The epithelium over the dorsum in the anterior region of the base is raised to form thick and well developed papillae. Finally at the base of the tongue on either side, a well developed lymph sac (Pl. 3, fig. 11) is present, which provides a mechanism for extrusion of the tongue in adult life.

Thyroid

In stage IV the thyroid diverticulum is seen in the floor of the pharynx (Pl. 2, fig. 9), caudal to the tuberculum impar, as a small median bilobed endodermal mass. By the next stage the lumen of the diverticulum is obliterated, and the thyroid gland is seen in the final stage as a median bilobed structure surrounded by a condensation of mesenchyme lying just below the floor of the pharynx.

Body cavity

The lateral plate mesoderm, derived from the primitive streak, proliferates bilaterally and follows the curve of the body wall between ectoderm and endoderm. By stage II it is approaching the mid-ventral line where it ultimately fuses to form a complete continuous tissue layer. In the dorsal regions, however, it has become separated into two layers to enclose a fairly wide coelom (Pl. 1, figs. 3 and 4), which eventually extends around the whole yolk mass. As a result of the formation of the body cavity, the lumen of the gastrocoele, which will form the definitive gut cavity, has become reduced and is now suspended in the midline by a thick dorsal mesentery.

Oesophagus

As a result of the formation of the body cavity, the future oesophagus has come to lie dorsally in the midline of the embryo, and at this stage is merely a narrow tube of endoderm enclosed at the sides by a layer of splanchnopleuric mesoderm. In stage III the endoderm of the oesophagus shows signs of proliferation, and by stage IV the lumen has been completely obliterated by cellular proliferation. Meanwhile the splanchnopleuric mesoderm which now lies on either side and ventral to the oesophagus, has thickened and is composed of fusiform-shaped cells, which differentiate into smooth muscle by stage VI. By stage IX the lumen of the oesophagus has been recanalised and the endoderm has differentiated to form stratified epithelium.

Fore-, mid- and hindgut

The development of the gut in *E. martinicensis* agrees with that described by Sampson (1904). In stage II the remainder of the gastrocoele shows regional variation indicative of the portion of the gut into which it will eventually develop. In stage III the cephalic portion has begun to dilate and form the stomach. The midgut region remains attached to the yolk mass and in continuity with it (Pl. 2, fig. 8). Meanwhile the body cavity has completely surrounded the yolk mass to form a ventral mesentery (Pl. 2, fig. 8).

In stage IV the proctodaeum has now extended to meet the caudal portion of the cloaca ; continuity occurs in stage IX (Pl. 3, fig. 12) when the cloacal membrane breaks down. By stage IX the proctodaeum is lined by stratified epithelium, and forms the definitive anal (cloacal) aperture (Pl. 3, fig. 12).

Liver

The primordium of the liver is present in stage II. By stage III it forms a massive structure and the endoderm has differentiated to form the typical liver structure (Pl. 2, fig. 7). In stage IV the bile duct becomes lined by a columnar epithelium. Lying on the ventral aspect of the liver, the gall bladder is seen as an elongated pear-shaped viscus lined by a high columnar epithelium and having a thick external coat. It is joined to the bile duct by a short twisted duct. From now on the liver undergoes further expansion in a bilateral direction until in the final stage it forms a large bilobed organ.

Pancreas

The pancreas arises from three separate rudiments, as described by Sampson (1904). By stage IX it is undergoing histo-differentiation.

The respiratory system

In stage IV the tracheal diverticulum extends downwards in front of the oesophagus, and the lung buds expand laterally into the cephalic portion of the coelom. By stage V a glottis has formed around the upper aspect of the trachea. The endodermal tracheal lining is differentiating, and the right and left bronchi are beginning to branch. The lung buds continue to expand, whilst the splanchnopleuric mesoderm has become thinned to form the pleura.

In the final stage the glottis architecture is completed and the tracheal lining is of columnar epithelium. In the ventral region of the glottis a small sac-like structure, the subgular sac, passes cranially. The bronchial lining is of columnar epithelium, but the actual lung substance is still composed of yolk endoderm and shows no signs of differentiation. The lungs are enclosed within the pleural cavity, since the diaphragm has now formed. Since the lungs are not functional for some time after hatching (Sampson, 1904) differentiation must continue and be a fairly rapid process.

The urogenital system

The rudimentary pronephros is present in stage II (Pl. 1, fig. 2) ; its tubules pass dorso-laterally to fuse and form the pronephric duct. An internal glomerulus invaginates the medial end of each tubule ; external glomeruli project into the dorso-medial aspect of the coelom. Both of these elements derive their blood supply from the aortic arches and dorsal aorta via the lateral segmental arteries. The tubules communicate through nephrostomes with the dorsal angle of the coelom. The tubules are lined by cubical epithelium, the nephrostomes by cilated columnar epithelium, and the internal glomerulus is covered by pavement epithelium. At this stage the pronephric region is small and limited to the extreme cranial portion of the nephrogenic mesoderm. It occupies some 50 μ of the total length of the mesoderm, and only two tubules are present.

By stage III four tubules of the pronephros have developed (Pl. 2, fig. 8), have undergone extensive dilatation and are coiled so as to form a compact organ. The pronephric duct passes caudally and then medially to meet its fellow in the midline, where they fuse prior to opening into the dorso-lateral aspect of the hindgut. The latter has a small lumen lined by flattened cubical epithelium and the whole is surrounded by condensed mesoderm. Further enlargement of the pronephros occurs in stage IV (Pl. 2, fig. 9), but the most cephalic tubule has become a solid mass prior to degeneration. In the remaining three tubules the nephrostomic channel is obliterated, and the cell lining shows evidence of degeneration, as is to be expected with the appearance of the mesonephros at this stage of development. By stage V only two tubules retain their lumen, and in the final stage the remnants of these are evident as a solid mass of heavily stained tissue at the upper pole of the mesonephros. The mesonephros develops from the remainder of the nephrogenic mesoderm, commencing at its caudal extremity. Several mesonephric tubules have developed by stage IV, and open medially into the pronephric duct. By stage V more mesonephric tubules have developed, and these now show dilatation and coiling. No nephrostomes or external glomeruli are formed in connexion with this organ. It increases in complexity and is supplied by a large single artery from the dorsal aorta, whilst the surrounding mesoderm has condensed to form a capsule. The pronephric duct, which now forms the mesonephric duct, is lined by a double layer of small cubical cells and the surrounding mesoderm has differentiated to form muscular coats.

The bladder appears in stage IX as a hollow bifid sac from the ventral wall of the cloaca (Pl. 3, fig. 12). The lumen of the sac is lined by a single layer of

cubical cells, and external to this a thin layer of smooth muscle is present. Communication with the cloaca is maintained through a very small circular orifice. At the lateral sides of the bladder the mesonephric ducts open into the cloaca.

The genital ridges are apparent in stage V as small localised thickenings of mesoderm at the cranial extremity of the mesonephros in relation to the degenerating pronephros. In the final stage no further development is noted, and the development of the gonads is thus deferred until the animal has a free existence.

The central nervous system

In stage I the future central nervous system is represented by a flattened plate of specialised ectoderm, i.e. the neurectoderm, which lies immediately in front of the neurenteric canal. By the next stage the axial neural groove, or in places, the neural tube, bent in conformity with the dorsal convexity of the embryo, has been formed (Pl. 1, figs. 2, 3 and 4). It is surrounded by a mass of loose undifferentiated mesoderm and terminates just within the developing tail. Differential expansion of the tube cranially to form the future brain may be noted, but the caudal third of the tube remains cylindrical in outline to form the spinal cord. Neural crest tissue is related to the dorso-lateral aspect of the neural tube.

Brain

The future brain region has become grossly expanded by stage III (Pl. 1, fig. 6), and the head region has flexed upon the yolk mass surface, to produce a marked ventral flexure at the junction between the brain and spinal cord. The expanded brain region shows division into the telencephalon, diencephalon, mesencephalon, metencephalon and myelencephalon. The mesencephalon forms a narrow limited region at this stage from which are developed the optic lobes and centres.

The telencephalon (Pl. 1, fig. 6) has initially thickened walls and floor plate together with a thin roof. As development proceeds the walls, floor and roof increase in thickness. The olfactory region expands cephalically and bilaterally as two diverticula, which form the bulb and tract. The olfactory lobes become depressed with the expansion bilaterally and caudally of the cerebral hemispheres. Owing to the caudal expansion of the cerebral hemispheres and the cranial expansion of the optic lobes, the diencephalic region, originally quite large (Pl. 1, fig. 5) becomes overlapped by these two elements. The third ventricle shows a cephalo-inferior prolongation to form the optic recess of the third ventricle. As development proceeds the walls and floor of the third ventricle become greatly thickened and encroach upon its lumen ; the roof, however, remains relatively thin and from it a small evagination arises to mark the site of development of the pineal stalk and body. Eventually the caudal portion of the roof is invaginated by invading blood vessels to form the choroid plexus.

The optic lobes (Pl. 2, fig. 9) arise as dorso-lateral expansions from the superior aspect of the mid-brain. As development proceeds they expand

cephalically to overlie the diencephalon, and caudally to cover the superior aspect of the hindbrain. They enclose a T-shaped lumen which inferiorly opens into the aqueduct.

The cerebellar primordia are present in stage III as thickened rhombic lips of the cephalic portion of the metencephalon (Pl. 2, fig. 7). Eventually they fuse, and the cerebellum comes to lie immediately caudal to the optic lobes.

The remainder of the hind-brain develops into the medulla oblongata, whose roof remains very thin (Pl. 2, fig. 8) and finally becomes invaginated to form the choroid plexus.

Spinal cord

The tubular outline of the primitive spinal cord becomes altered in stage III with the appearance of the alar and basal laminae. Later they fuse partially, and the lumen of the tube is considerably reduced to that of the narrow central canal. In the earlier stages the spinal cord extends well into the tail region, but as the latter degenerates the caudal part of the cord undergoes de-differentiation and regresses.

In stage VI dorsal and ventral rootlets are seen connecting the cord and the dorsal root ganglia which were formed from the neural crest in stage III.

Histogenesis

The medullary epithelium is composed of several cell layers, the cells being columnar in shape, possessing a central spherical nucleus. Along the lumen of the ventricular system the germinal cells of the medullary epithelium show great mitotic activity. By stage IV the ependymal, mantle and marginal zones are identifiable.

The cytoarchitecture of the optic lobes is complex, and shows seven histological layers.

Spinal ganglia

The spinal ganglia develop from the neural crest and are present in stage III of development. They consist of a mass of rounded cells surrounded by condensed mesoderm. As development progresses they increase in size, and the mesoderm differentiates to form a capsule.

Special ganglia

In the head region in stage III, four rounded clumps of cells are present on either side. These are the sensory ganglia of the fifth, seventh, eighth, ninth and tenth cranial nerves (Pl. 2, fig. 7). The seventh and eighth are associated as the acoustico-facial complex which lies in medial relation to the otocyst. In stage V connexion between the latter is evident.

Pineal gland

In stage III the pineal diverticulum passes cephalically from the roof of the diencephalon ; it later elongates and becomes solid due to cellular proliferation at its cephalic extremity. By stage IX the solid mass forms the spherical pineal body, but the stalk still remains hollow and communicates with the third ventricle.

Pituitary gland

The nervous part of the pituitary is seen in stage III as an evagination from the floor of the diencephalon. This is met by a corresponding ectodermal evagination (Rathke's pouch) from the roof of the primitive buccal cavity in stage IV. By stage V the two components have fused and form a solid mass in relation to the diencephalon ; the connexion between the buccal cavity and the pituitary does not persist. In stage IX the pituitary has begun histo-differentiation, and the stalk which connects it to the diencephalon has become solid.

The eye and accessory structures

The primordium of the eye appears in stage II as a diverticulum from the lateral aspect of the prosencephalon. Development proceeds rapidly and by stage III the optic cup has been elaborated and a lens is present (Pl. 1, fig. 5). The two layers of the optic cup have approximated, and considerable expansion of the whole primordium has resulted in its protrusion from the lateral aspect of the head. By stage IV the surrounding mesoderm has started to differentiate into the very vascular choroid and sclera. The lens cavity has become obliterated, and the eye has undergone further expansion. The retina shows histo-differentiation into pars nervosa and pigmented layer in stage V. Condensation of the lens has occurred, and it shows a well formed compact homogeneous capsule, whilst the substantia propria of the lens has a laminated structure. In stage VI the fibres from the retina have begun to pass backwards along the optic stalk and by the next stage they reach the brain after forming the optic chiasma. In the final stage the retina shows the typical six structural layers, and the rods and cones are present. A retractor muscle is attached to the bony orbit and the upper pole of the eyeball.

The eyelids appear in stage III as ectodermal folds enclosing a layer of mesenchyme. By stage IV the free edges have approximated and thus cover the free surface of the cornea (Pl. 3, fig. 10). Throughout development and adult life they remain unpigmented.

Ear

By stage III the otic placode has sunk into the underlying tissue to form the otic vesicle, with the acoustico-facial ganglion close to its medial aspect. In subsequent stages the endolymphatic organ is formed from the otocyst. The middle-ear cavity arises from the dorsal part of the second pharyngeal pouch, and the columella is formed from the dorsal portion of the second arch cartilage.

Nose

The nasal placode forms at the antero-lateral margin of the stomodaeum in stage II. In stage III, an olfactory pit develops (Pl. 1, fig. 6) and this diverticulum meets with one from the internal aspect of the stomodaeum to form the nares by stage IV. The cavity of the nostril (Pl. 3, figs. 10 and 11) develops several side chambers and is medially closely related to the olfactory nerve. Several mucous glands develop along its length.

Tail

The rudiment of the tail is present in stage II as a compact cylindrical mass with lateral expansions. The notochord forms the axis of the tail, and already numerous capillary-like spaces within its substance suggest the development of blood vessels. In the next stage the organ has undergone prolific expansion (Pl. 2, fig. 8) ; it is highly vascular and serves as a respiratory organ. From stage V onwards (Pl. 3, fig. 12) the tail shows signs of degeneration, coincidental with the accession of the skin to the role of embryonic respirator.

External gills

External gills are present in stage III as a fold of vascular ectoderm between the head and fore-limb (Pl. 2, fig. 7) ; they are transitory elements, however, since they disappear in stage IV. Noble (1927) has described transitory external gills in two species of *Eleutherodactylus* and Lutz (1947) in " one group of species ", but neither mention *E. martinicensis* as being one of them, although Bavay (1873) reported transitory external gills in *E. martinicensis*, appearing on the fourth day and lasting until the seventh.

Limbs

The fore- and hind-limb buds appear simultaneously in stage II, and are composed of a condensed mass of mesoderm over which the surface ectoderm has become thickened (Pl. 1, fig. 2). All three segments of the limbs are established by stage IV. The hind-limbs are flexed and drawn up close to the lateral side of the body, while the fore-limbs are directed anteriorly between the head and yolk mass, and remain in such a position until development is completed. Meanwhile the condensed central portion of the mesoderm has undergone further condensation and has differentiated to form the precartilaginous blastemata of the limb bones. The bones of the middle segment of the limbs develop as separate entities, despite the fact that they become fused in the next stage. The cartilaginous precursors of the limb bones are present in stage V, and the surrounding mesoderm has begun to differentiate to form the voluntary musculature. Coincidental with this the precursors of the pelvic and pectoral girdles are laid down. Ossification commences in stage VII, and the joint cavities are completed by stage VIII.

Skin

In stage III the surface ectoderm is thickened and numerous ciliated columnar epithelial cells have appeared whose function is to provide the impetus for rotation of the embryo within the egg membranes. By the next stage the ectoderm has differentiated into a multicellular layer composed of cubical cells whose outer layer is covered by a continuous cuticular deposit. The mesoderm, now composed of undifferentiated mesenchyme is very vascular, containing many small blood vessels whose lumina are packed with nucleated blood corpuscles. Pigment is first deposited in the mesodermal zone in stage IV, and from then until hatching there is a marked increase in deposition.

Lymph sacs

Subdermal lymph sacs appear in the final stage. The ventral sac extends the full length of the embryo producing pouching of the skin under the jaw (Pl. 3, fig. 11).

Egg tooth

The egg tooth is seen as a mass of ectoderm on the tip of the snout in stage VII. It is deeply pigmented and eventually becomes cornified (Pl. 4, figs. 13 and 14).

Yolk mass

At hatching a considerable amount of yolk endoderm remains, and forms the nutriment in early adult life. Throughout development it is gradually reduced and shows division into an outer zone of small cells which form the immediate nutritive source, and a central zone of larger cells.

DISCUSSION

Elimination of the tadpole stage is by no means unique to the genus *Eleutherodactylus*, and many other diverse forms of early development among the amphibia are commonly found. In fact in all three orders there are exceptions to the rule that they must develop from eggs laid in water and pass through a free-swimming larval stage until metamorphosis takes place.

The use of the tail as a respiratory organ is probably over-emphasized since the skin soon becomes extensively vascularized after the tail begins to degenerate. Further onus is thrown on the respiratory function of the skin by the fact that the lungs only become functional after birth.

The incomplete differentiation of the gut at birth appears to be in conformity with the large amounts of nutritive yolk present in the newly-hatched animal.

The lack of complete elaboration of unessential organs is reflected in the absence of sex differentiation before hatching, and is to be expected in cases in which development ensues rapidly. In fact the whole process of development seems to be adapted for producing an animal which can just survive in its environment, and the later development in the free frog of other features which are not essential for survival. Further, the process of development illustrates excellently the general trend of modified salientian ontogeny towards withdrawal of development from water (Lutz, 1948), correlated with increasing yolk reserves and avoidance of double development by absence of a free-swimming larval stage. There is also some similarity between the development of *Eleutherodactylus* and *Leiopelma* (Stephenson, 1951).

The presence of an egg tooth is an interesting feature of this frog, which is obviously correlated with the method of development in a tough egg case ; Noble (1926) has described it as a well-developed horny layer to the epidermis lying directly over the symphysis of the premaxillae in all species of *Eleutherodactylus* he investigated. The method of mechanical rupture of the egg membranes by an egg tooth seems to be constant for all Salientia with direct development. The form of the tooth also differs ; in *E. abbotti* it has the appearance of a pair of " bulls ' horns " in miniature, while in *E. inoptatus*

the egg tooth is very small and hatching must be initiated by rainfall. In *E. martinicensis* the tooth (Pl. 4, figs. 13 and 14) is a spherical mass of epidermis appearing on the seventh day and becoming cornified by the eighth day, but it is very likely that hatching can occur without the tooth. The egg membranes become more brittle as hatching approaches and movement only of the tail (as in *Leiopelma*) and legs is probably sufficient to enable hatching to occur—on occasions as early as the eighth day of development, particularly if there are dry conditions ; in fact there is much evidence to suggest that hatching in *E. martinicensis* occurs most favourably in dry conditions. The eggs are usually laid after heavy rain following a drought ; such rain is frequently followed by a dry period again within nine days so that the eggs will be dry by the time of hatching. This is also ensured by the frog laying its eggs in a well-drained site ; indeed if they remain moist throughout the whole period of development the eggs grow fungus. Experimental addition of water to the eggs two days before the normal time of hatching causes the egg membranes to swell enormously and hatching may be delayed until the 11th or 12th day. A constant phenomenon is for the female *E. martinicensis* to urinate over her eggs if disturbed during the period she stays with the eggs.

In *Rana opisthodon* de Beer (1949) described an epidermal spike at the very tip of the snout supported by a massive median cartilaginous rostrum extending forwards from the skull in a manner unique in the Anura. This structure is clearly not homologous with the epidermal caruncles of *E. martinicensis* and *E. abbotti*.

No trace of lateral line canals or organs (see Escher, 1925) could be found at any stage of development in *E. martinicensis*.

Since almost complete development occurs during the period the embryo spends in its transparent " shell ", it would be of immense value for teaching purposes. Unfortunately attempts to make the frog ovulate in captivity in Liverpool, even using injections of chorionic gonadotrophin into the dorsal lymph sac, have failed, although the adult frog lives quite happily in the artificial environment of a vivarium.

SUMMARY

The development of *Eleutherodactylus martinicensis*, as observed histologically and by microscopy of whole cleared specimens, is described and compared with that of other frogs. The most remarkable feature of the development is the almost complete metamorphosis over a period of 10 days within the egg membranes, the frog eventually liberating itself by means of an egg tooth. The frog develops transitory external gills and has a tail which is also transitory, and subserves a respiratory function.

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EXPLANATION OF PLATES

PLATE 1

Fig. 1.—Transverse section of the roof plate (r.p.) of a stage I embryo, showing the evagination of the gastrocoele (g) meeting the primitive groove (p.g.). The yolk (y) is lying ventral to the gastrocoele. × 95.

„ 2.—Transverse section of a stage II embryo to show the neural tube (n.t.), fore-limb bud (f.l.b.), pronephros (p) and primitive heart tube (h.t.). × 75.

„ 3 and 4.—Oblique transverse sections of stage II embryos demonstrating the neural folds (n.f.), gastrocoele (g) and coelom (c). × 85.

„ 5.—A stage III embryo in transverse section in the region of the stomodaeum (st.) and diencephalon (di.), demonstrating the optic cup (o.c.), lens (l), maxillary (max. p.) and mandibular (m.p.) processes, and dividing conus arteriosus (c.a.). × 80.

„ 6.—A transverse section of the head end of a stage III embryo cephalic to Fig. 5, showing the telencephalic vesicles (te.) and the nasal placodes (n.p.) in the nasal pits. The vitelline vein (v.v.) can be seen on the surface of the yolk.

PLATE 2

Fig. 7.—The pharynx (ph.) of a stage III embryo shown in transverse section lying ventral to the metencephalon (met.) whose lateral wall shows the beginning formation of cerebellar swellings. Lateral to the metencephalon lie the sensory ganglia of IX and X (ga.), while lateral to the pharynx an external gill (e.g.) is visible. The sinus venosus (s.v.) and atrium lie dorsal to the cephalic end of the liver (li.) and vitelline vein (v.v.) on the surface of the yolk. × 55.

Fig. 8.—A more caudally situated transverse section of a stage III embryo showing the medulla oblongata (m.o.), pronephros (p.), mid-gut (m.g.) in continuity with the yolk (y), and hind-gut (h.g.) with its ventral mesentery (v.m.). The tail (ta.) and ectoderm (e.) of the embryo are also visible. × 45.

„ 9.—A paramedian section through the head of a stage IV embryo showing a telencephalic vesicle (te.) and an optic lobe (o.l.). Meckel's cartilage (m.c.) has formed in the mandibular processes, and the tongue (t.) and thyroid diverticulum (t.d.) are visible in the floor of the mouth. The hypophyseal fossa (h.f.) and pronephros (p.) may be seen. × 60.

PLATE 3

Fig. 10.—A section through a stage IX embryo cutting the head end and spinal cord (s.c.) showing the optic cup (o.c.), eyelids (e.l.) and external naris (e.n.). The liver (li.) and mid-gut (m.g.) are also visible. × 32.

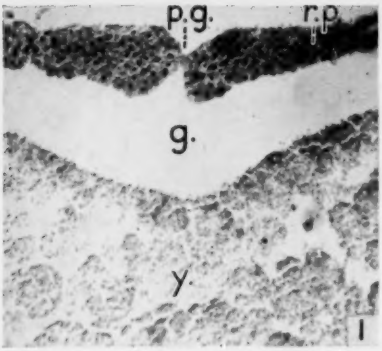
„ 11.—An oblique transverse section through the head end of a stage IX embryo to show the tongue (t.) with its retractor muscle (r.m.), the external naris (e.n.) and nasal sinus (n.s.). The dorsal (d.l.s.) and ventral (v.l.s.) lymph sacs are well shown, as also the olfactory lobes (o.l.). × 45.

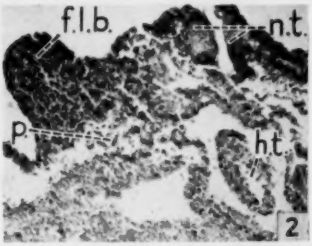
„ 12.—Histological section through the tail end of a stage IX embryo showing the degenerating tail (ta.), anus (a.), cloaca (cl.), mid-gut (m.g.) and hind-gut (h.g.). × 55.

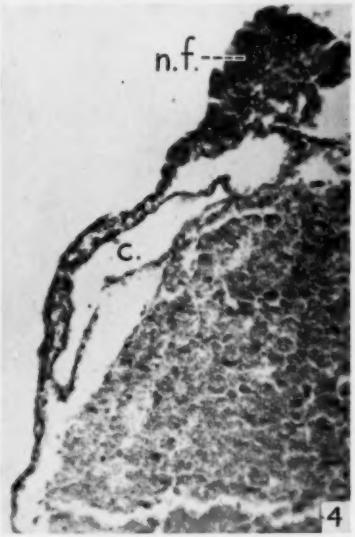
PLATE 4

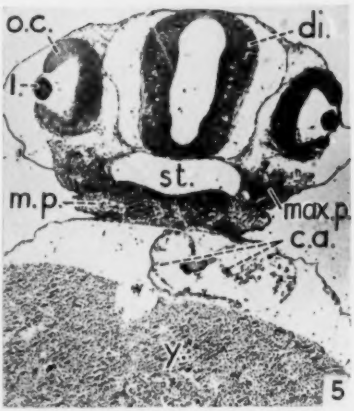
Fig. 13.—A paramedian section through the head end of an 8-day embryo to show the egg tooth (e.t.) lying just above the upper jaw margin (j.m.). × 280.

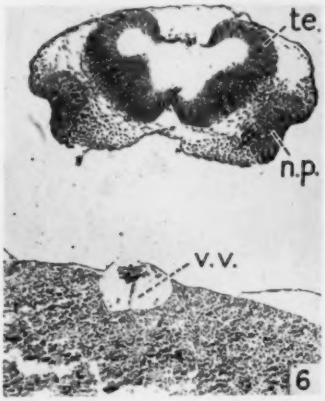
„ 14.—A high-power view of the egg tooth shown in Fig. 13. It can be seen to be composed of a knob of proliferated epidermis covered by a cap of cornified cells. × 1360.



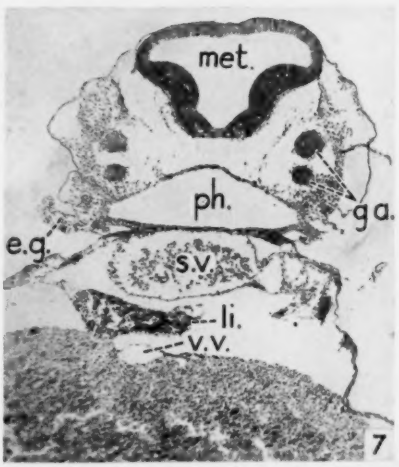


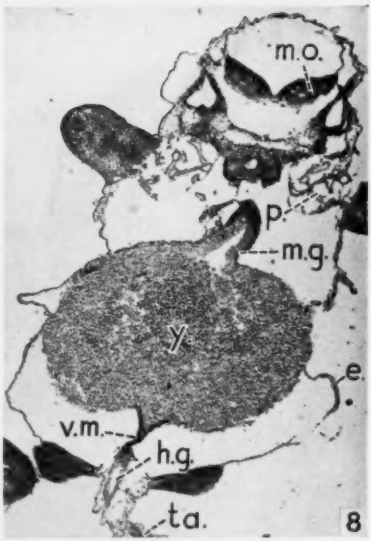


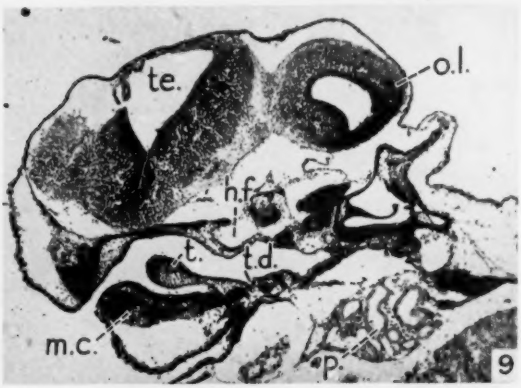




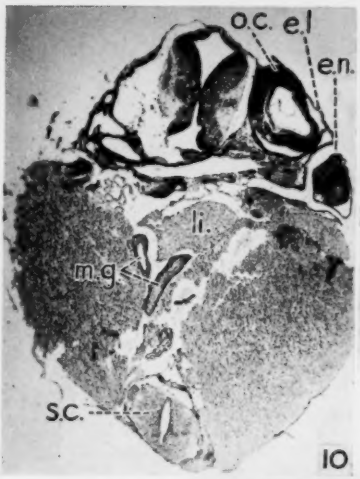
The development of the Whistling Frog *Eleutherodactylus martinicensis*.

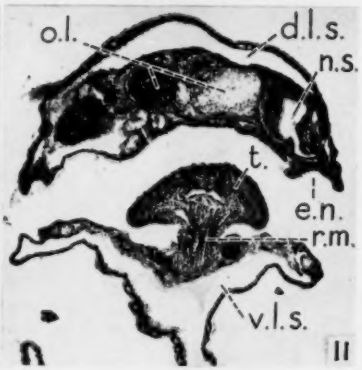


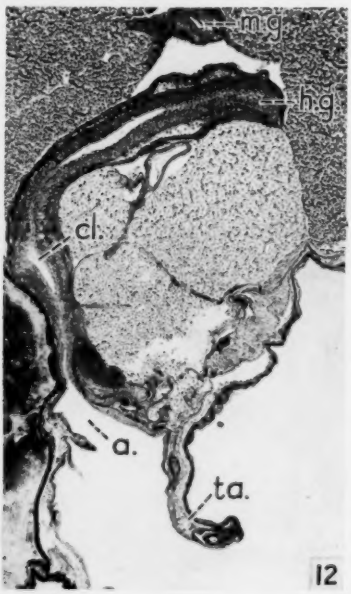




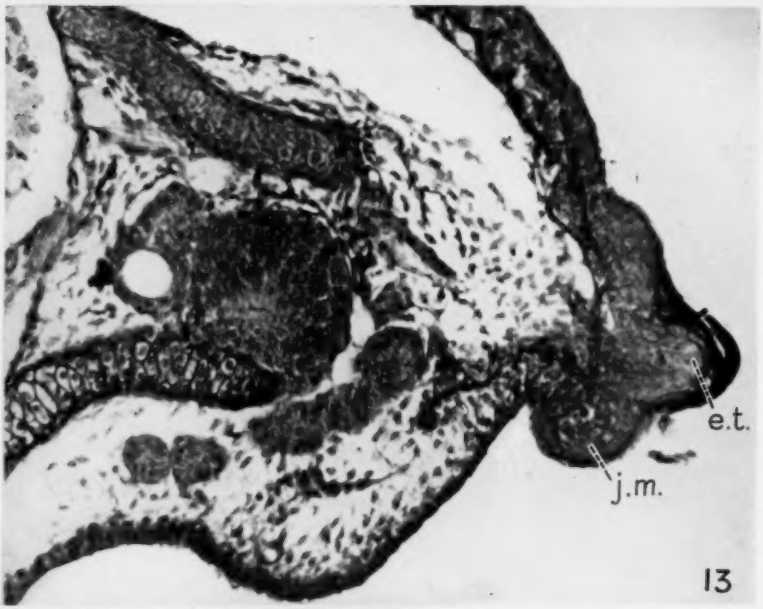
The development of the Whistling Frog *Eleutherodactylus martinicensis*.

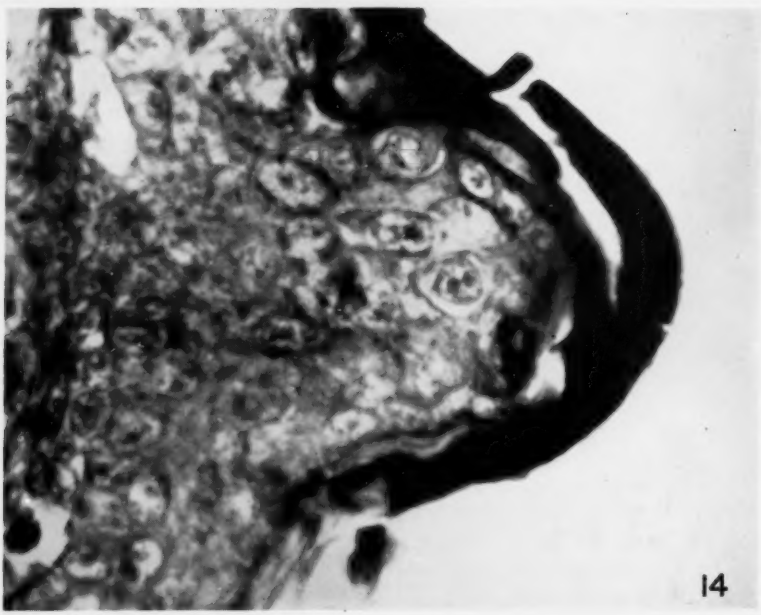






The development of the Whistling Frog *Eleutherodactylus martinicensis*.





The development of the Whistling Frog *Eleutherodactylus martinicensis*.

OBSERVATIONS ON *ARGONAUTA* AND ESPECIALLY ITS METHOD OF FEEDING

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[Accepted 12th May 1959]

(With 2 plates and 2 figures in the text)

CONTENTS

	Page
Introduction	471
Locomotion	471
The arms	472
The web	472
Feeding	473
Colour	475
Respiration	476
Ink	476
Leaving the shell	476
Significance of the shell and its web	477
Summary	479
References	479
Explanation of plates	479

INTRODUCTION

The Paper Nautilus, *Argonauta argo*, is from time to time brought alive to aquaria and there have been various reports of its behaviour during the one to two weeks that it has been kept alive. Nevertheless much remains obscure about this extraordinary pelagic octopod, and especially the use of its shell and the silver membrane that covers it. The following observations were made on a female that was caught close inshore in July 1957 near Mergellina harbour and brought at once to the Naples station, and lived, apparently in good health, for seven days. During this time it fed regularly and laid two batches of eggs. It twice left the shell but, with assistance, readily returned.

The argonauta was kept in a glass-sided tank with good daylight illumination (but not full sunlight) to allow photography. The water was well aerated by a jet. The animal did not seem either to seek or avoid the lighter or more shady parts of the tank.

LOCOMOTION

When first brought in there was much air in the apex of the shell and the animal floated all the time at the surface, with the top of the shell well above the water. Some of the air came out readily when the shell was tilted by hand. In the later days the amount of air in the shell was usually just enough to hold the animal floating at mid-tank level.

The argonauta often came to the surface and also went to the bottom. Sometimes there would be more air in the shell so that it again floated with the top of the shell out of the water. It was not clear whether this air was secreted or came from the bubbles of the inlet jet, nor how it was removed by the animal.

Movement was entirely by the funnel, which is kept protruded between the ventral arms and in general drives the animal upwards and backwards. Swimming is clumsy and slow. The funnel can be turned sideways and perhaps upwards, but there was little steering. The more dorsal arms were sometimes spread out as a horizontal stabiliser, but the motion was always rocky and irregular. There was no clear sign of forward swimming except for the very short distances described later under " feeding ".

The argonauta frequently held on to the glass sides of the tank with the suckers around the mouth, less often to the white marble bottom of the tank.

THE ARMS

Argonauta sits in its shell with the arms turned backwards, presenting the suckers and beak forwards (Pl. 1). The ventral three pairs of arms have their distal ends turned back within the shell, except when they are pushed out for feeding (see below). The most dorsal (first) pair of arms may also be within the shell, but they are provided with an extensive web, which can be spread out over the whole surface of the shell.

THE WEB

The web is a very thin flattened extension of the dorsal side of the first pair of arms. Since the arms are turned backwards the web hangs ventrally on the shell. It may be spread out over the whole surface of the latter but is often withdrawn and wholly concealed within. The first sign of its reappearance is as a shining white mass near the apex of the shell. This then spreads ventrally as a silver stream, pouring steadily over the shell and covering it in about 15 seconds (Pl. 2). Red chromatophores begin to show when the main dorsal part is extended. The extreme dorsal edge of the shell is covered last, by the extension over it of the proximal portion of the arms, coloured intensely blue.

The extension of the web is achieved mainly, perhaps wholly, by the suckers of the arm, creeping over the shell. The lower and anterior border of the shell is however covered by the dorsal edge of the web, which is without suckers and it is not clear how the final stages of extension are achieved. The whole movement proceeds in an uncannily steady manner so that the shell is covered before one realises what is happening.

When the web is out the whole surface shows a brilliant white iridescence (Pl. 1). The upper part is tinged with red from chromatophores, arranged in circular groups. The lower part is a shining silver white. The suckers and surface of the uppermost edge are brilliant blue, the deep blue suckers making a pattern of darker lines.

The veins on the arms (first observed by Lacaze-Duthiers in 1892) appear very clearly and centripetal peristaltic waves pass along them. This movement

is sufficiently conspicuous to give a shimmer to the iridescence of the whole web.

There was no clear periodicity in the emergence of the web. For long periods it would be withdrawn and then appear on one or both sides and remain spread for a long time. It appeared both at day and night, perhaps mainly in the day. Sometimes after being withdrawn it would appear again almost at once ; or it might remain inside for hours on end.

If the animal was strongly stimulated by a rod the web was suddenly withdrawn. The effect produced is first of a brilliant shining silver patch on the side of the shell, which then disappears as the web is pulled inside. The effect could well produce a startle reaction in an attacker and is thus to be classed as a dymantic reaction (Young, 1950). This sudden withdrawal was sometimes seen when a large object moved in the visual field.

The web was often spread out on the glass sides of the tank. It would then adopt the full curved form of the shell and showed its characteristic colours and the pulsations in the veins. The use of the suckers in spreading out the web was very clearly seen on the glass. Sometimes the whole web moved slowly forwards over the glass, dragging the animal after it. Presumably this attachment to foreign surfaces never occurs in nature and the suckers normally stop moving when they reach the edge of the shell.

FEEDING

A piece of dead sardine placed in the arms was seized and transferred to the mouth. The beak immediately began to gnaw it and much was eaten. However, clouds of pieces also appeared and were blown away by the funnel, as if the feeding were a wasteful process. The argonauta would nearly always seize and eat sardines in this way, but never finished any piece it was given ; sooner or later it was dropped. Sardines attached to a piece of thread and waved 5–10 cm. in front of the animal produced clear reactions. The chromatophores around the eyes darkened. Mantle movements were increased and the funnel was directed to the opposite side so that the argonauta turned to face the fish. Meanwhile the ventral part of the body was protruded and the ventral two pairs of arms were rolled out towards the fish. They were never seen actually to shoot out to their full length but often seemed to be about to do so. If the fish came near enough it was seized by the partly protruded arms.

The argonauta would turn towards a fish and push out at it, with perhaps some puffs of the backwardly directed funnel to bring it nearer, but without any clear " attack ". However the impression that an attack was imminent was often strong and it may be that under natural conditions, *Argonauta* moves actively forward to seize prey with the ventral arms.

The argonauta made no attacks on small fishes swimming in the tank. Nor would it attack a prawn, attached to a string and drawn past it. If the prawn touched the arms it was rejected without any signs of handling movements such as a *Sepia* would show.

Definite feeding reactions were shown when pieces of fish touched the extended web. The ventral arm of the appropriate side was put out and swept upwards over the web until the fish was seized (Pl. 2). This reaction was elicited many times and is undoubtedly one of the functions of the web. The

edge of the web and suckers are the most sensitive parts, but the reaction was also elicited from contact of the fish with the flat part of the web.

A very clear demonstration of this feeding reaction was obtained when the web was fully extended on the glass side of the tank, but *in front* of the body of the animal (Fig. 1). If a piece of fish was now touched against its surface the fourth arm of the same side was pushed out and swept backwards and

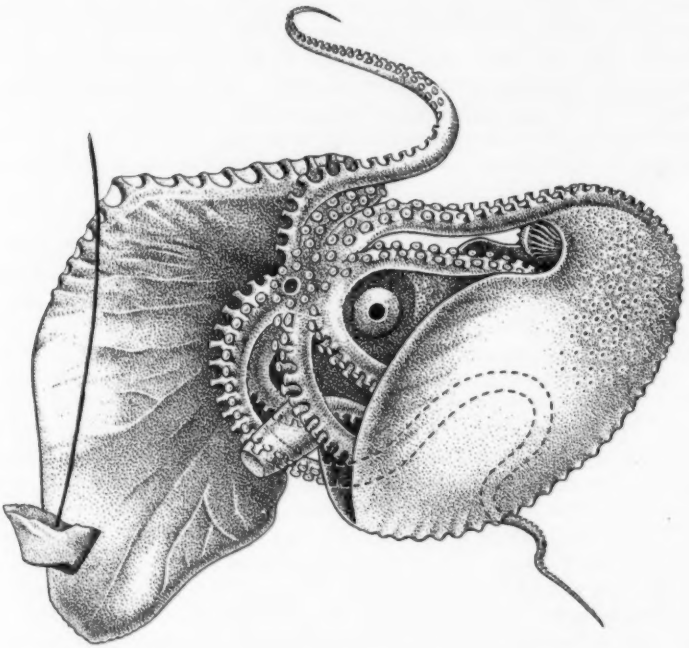

Fig. 1.—Drawing to show experiment made when the web was spread out on the side of the tank. Food touched against its outer surface elicits a backward movement of the fourth arm, sweeping the place where the web should have been on the shell.

upwards *over the shell*. That is to say the arm was extended backwards away from the food, and therefore not over the web, which was in front of the animal. Needless to say this movement did not result in seizure of the fish. It demonstrates that the effect of contact of food with the web is to elicit a fixed action pattern, by which the fourth arm sweeps up over the shell—where the web and food would normally be found.

A curious reaction observed several times after feeding was that the argonauta went to the bottom of the tank and attached itself for a few seconds there. It was not obviously picking up any pieces. Possibly this downward movement after feeding is protective—but it remains obscure.

These observations show only that under artificial conditions argonauta will feed on dead fish but not on shrimps. Pieces of fish moving nearby are " attacked " and the web is used as a receptor to detect the presence of food. This suggests that *Argonauta* eats such food as touches it while it drifts in the plancton. The swimming is so slow and inefficient that it is difficult to believe that any swift movements of attack on distant prey are possible. It may be that the animal is more active under normal conditions, but for much of the time in the laboratory it seemed to be in good health.

COLOUR

When swimming with the web out *Argonauta* in lateral view shows a shining irridescence, white over most of the shell but purplish-red over the upper part of the web (Pl. 1). The proximal suckers of the first pair of arms showed a brilliant blue when the animal first came in to the laboratories, later they were more purple. The ventral surfaces of the arms are all turned outwards and upwards and they and the webs between them show the same iridescence as the main web, that is to say white on the ventral arms (3 and 4) purplish blue on the dorsal ones (1 and 2). The whole under part of the animal is thus shining white, the upper part, at the water surface is purplish blue, except for the white of the suckers.

The eye shows very conspicuously, with a jet black, round and unvarying pupil. The iris around the pupil is iridescent steely blue-white, with red and blue chromatophores, especially over the dorsal half of its circumference. These chromatophores readily expand when there is a sudden change in the visual field. The dorsal surface of the eye and the eye-stalk are very deeply pigmented with purple-blue chromatophores.

The skin of the funnel, neck and mantle is white and iridescent, but shines less brightly than the web. It carries sparse purple-red chromatophores, which expand when the animal is disturbed.

The beak is a deep blue-black colour. Seen from in front *Argonauta* therefore has a striking appearance with the dark patches above the eyes on either side and the beak at the centre, surrounded by white suckers on a purple background.

Although the colour is very striking the range of colour patterns produced is limited, far more so than in *Octopus*. When floating near the surface the coloration is cryptic, shining white below, darker above and with a broken line of blue near the water surface. The dark pigmentation of the tip of the shell contributes to this dark colour of the upper surface. When the animal is disturbed this pattern is varied by the expansion of more red chromatophores of the upper part of the web, arms, eyes, head, funnel and mantle. The only other definite colour pattern produced is the sudden flash of white as the web is withdrawn, probably serving as a dymantic pattern (see above). The colour of the animal was predominantly blue when first brought in but became more purple after living some days in the full light of a glass-sided aquarium.

RESPIRATION

The argonauta breathed continually, expanding the mantle to let in water through the valves behind the eyes and expelling it through the funnel, curled slightly forwards and downwards. The breathing was often very vigorous even when the animal had long been at rest in a current of bubbles from the inlet. At other times it was less 'forced'. Counts when the animal was breathing steadily gave 46, 47, and 46 beats in thirty seconds.

When the argonauta was handled the respiration stopped momentarily and began again more vigorously on release.

INK

The argonauta could be turned upside down to let out the air without ejecting ink. Once when it was strongly handled a feeble puff of ink appeared.

LEAVING THE SHELL

The argonauta twice left the shell, the second time shortly before dying. On neither occasion was the actual emergence seen. The first time the animal was found lying near the bottom with its webs spread out on the glass and the shell floating separately at the surface. The webs showed their full normal shape and the movement of the suckers by which they are held expanded could be especially well seen. The veins were fully active.

The movement of the web along the glass shifted the animal slowly, but no other effective locomotion was seen. Picking up the argonauta was difficult, because the arms held on to the bottom (and to one's fingers). When dropped free in the water the animal sank helplessly, making no effective efforts at locomotion. It is difficult therefore to believe that it could survive away from its shell, or that it could find it again and re-enter once the two had become separated.

However, when the animal was placed with the mantle within the shell it rapidly re-orientated itself in the proper position and shortly afterwards put out the web over the shell and resumed its normal life. It was not evident that there were any ill effects of the separation from the shell. After the animal had returned it ate fishes placed in contact with it, as it had done before, and lived afterwards for three days.

When the animal had left the shell eggs were seen to have remained behind, hanging from the dorsal edge of the coil. After the argonauta was returned to the shell the eggs became displaced (not during the actual process of putting back) and were found lying on the bottom of the tank.

On the second occasion of leaving the shell the animal was seen to be healthy at 9.00 and at 12.00 was lying on the bottom of the tank as before. The shell was again floating at the surface carrying a further mass of eggs. Before the argonauta could be replaced it stopped breathing and died.

The fact that eggs had been laid shortly before the animal left the shell raises the possibility that this is a normal process, since female octopuses die after laying and caring for their eggs (Vevers, 1960).

SIGNIFICANCE OF THE SHELL AND ITS WEB

Much has been written of the possible evolutionary origin and significance of the shell, with its striking similarity to that of an ammonite. Although an argonauta can leave its shell and return there is no doubt that the shell is essential for its life. Without it the arms assume no well co-ordinated positions and the animal is unable to swim or walk. Its first function is thus to co-ordinate the posture and locomotion of the argonauta. The air that is contained in its apex adjusts the specific gravity of the whole animal, allowing it to float in the water with a minimum of swimming effort. Other related planctonic octopods such as *Tremoctopus* and *Ocythöe* presumably expend more effort to maintain their position. On the other hand the presence of the shell makes rapid and well-directed swimming difficult, whether for seeking food or escape. There is no adequate information about the depths at which *Argonauta* is found. The coloration, as well as the flotation by the shell and the poor swimming suggest that it mainly drifts near the surface, but is capable of descending.

The primary function of the web may be regarded as production of the shell, by means of the glands set along its edge (Naef, 1923). Nevertheless it has clearly marked functions also in feeding and colour display. The reaction by which the ventral arms are put out to collect food that touches the web is very definite and readily elicited and must play a large part in the food collecting system of the animal. It is impossible at present to say whether it is the main or even exclusive method. In spite of repeated attempts it was not possible to make the argonauta shoot forward and project its arms to seize food, though it frequently seemed about to do so. (p. 473). The evidence is decisive that *Argonauta* takes food that comes in contact with its web or arms and it remains to be shown whether it can also make " attacks " such as those of other cephalopods. The fact that the eyes showed no movements and no signs of accommodation or variation in pupil diameter suggests that there is little active pursuit of food. Nevertheless the animal was seen to change colour when a fish was near and to turn towards it.

The protective functions of the web are probably both cryptic and dymantic. Its iridiscence is part of the general scheme of colouring common to animals living near the water surface. The sudden flash of white produced as the web is withdrawn seems to be a special adaptation protecting both the whole animal and the exposed soft surface from an attacker by startling it to flight.

A further function of the shell is to provide for the attachment of the eggs. This is a problem that is solved differently by each of the pelagic octopods. In all of them the extraordinary sexual dimorphism, with dwarf males and an autotomised hectocotylus is presumably a reaction to the difficulty of bringing males and females together at the right time is a pelagic environment. In *Tremoctopus* the eggs are apparently attached to the arms or possibly placed in the sacs on the head, *Ocythöe* retains the eggs within the oviduct. In *Argonauta* they are attached to the shell and can be oxygenated by the mother as conveniently as if they were fixed to a rock.

The question remains—how did this state of affairs arise? An incipient shell would have been no use either for support in the water, or to hold the web

as a food gathering area, or for the eggs. There seems no reason to reject the suggestions that these animals have evolved through a stage in which they lived within the discarded shells of others, fantastic as this may first seem (see Naef, 1923). Octopods commonly enter any cavity they can find. Moreover, they readily adopt a ' defence posture ' in which the arms are turned back to hold on to the walls of the crevice, with the suckers displayed outwards (Fig. 2). This is essentially the position adopted by *Argonauta* in its shell. It is not at all difficult to imagine that a race of octopods should adopt the habit of living within cast-off shells, as hermit-crabs do. Indeed the male

Fig 2.—Drawing of *Octopus vulgaris* within a small cavity.

Ocythöe is said to inhabit empty salp tunics. Once admitted this possible origin for the group it is tempting to speculate further as to *which* shells may have been the substrate, later abandoned as the argonautas made their own shells.

As Naef points out shells of ammonites and perhaps nautiloids must have been readily available in the Cretaceous and then gradually less so. The protoargonauts may have used them to protect themselves and their eggs as they swam to the surface and spread out their webs to catch food. Once a basic model shell was available the octopod could enlarge it with its own secretion and ultimately dispense with it altogether. The other pelagic octopods may even possibly have passed through a shell-living phase and adopted other means of food-gathering and egg protection when the supply of shells failed. The webbed arms of *Tremoctopus* though often rolled up can probably also be trailed in the water and may serve for food gathering. As Kramer (1937) has shown they may be broken off as 'handkerchiefs', waving in the water to distract an attacker, a function that recalls the startling effect recorded above for the withdrawal of the web of an argonauta (see also Portmann, 1952 Sacarrão, 1951).

There is no means at present available to prove that the Argonautidae once inhabited the shells of other animals. It may be possible, though difficult, to imagine that their shells have originated without such a precursor. In any case the hypothesis has value in drawing attention to the possible significance of the similarities and differences between the members of this extraordinary family of pelagic animals. Above all we need to know more facts about them.

SUMMARY

1. The behaviour of a female *Argonauta* kept alive for a week at Naples is described.

2. The animal usually swam near the surface but was capable of going down to the bottom and of attaching itself to the floor or sides of the tank.

3. The web is suddenly retracted from the shell when the animal is disturbed The resulting white flash produces a startling (dymantic) effect, causing flight of an attacker.

4. When a dead sardine was placed near the argonauta there were colour changes, quickened mantle contractions and movements of the arms, but no definite forward swimming or attack.

5. When a food particle touches the web the fourth arm of that side is brought out with a sweeping movement that captures the food.

6. No reactions were seen to live fishes or crustaceans.

7. On several occasions the argonauta spread out its web upon the glass side of the tank. The animal twice left the shell and then lay helpless. When re-placed in the shell it recovered completely on the first occasion but died upon the second.

8. Eggs were laid in the shell on both occasions before the animal left it.

9. The web and shell thus serve many purposes. The shell provides protection and flotation and allows attachment of the eggs. The web, besides secreting the shell, acts as a receptor for the feeding reaction, and provides a startling colour when the animal is disturbed.

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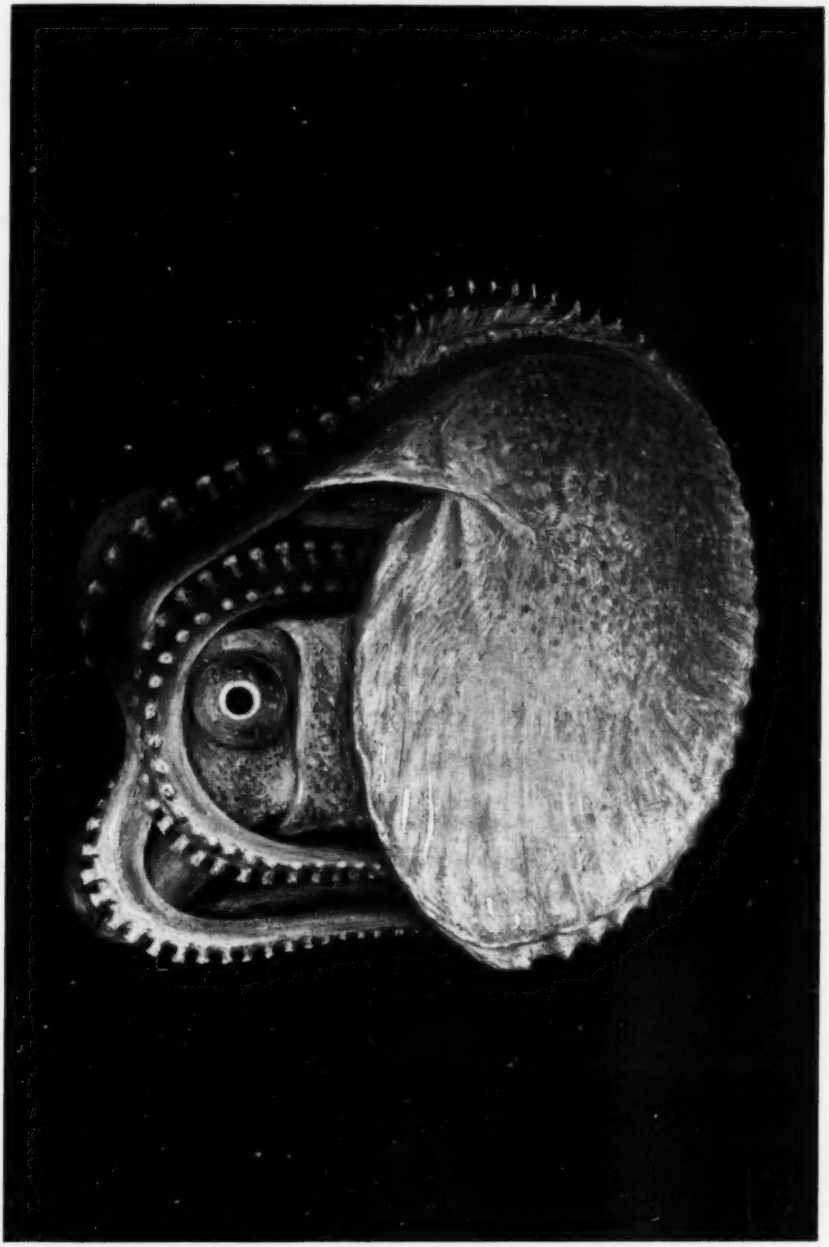
EXPLANATION OF PLATES

PLATE 1

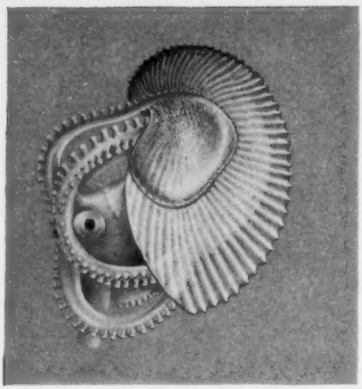
Female *Argonauta* in life. Painted by Miss J. de Vere from a coloured film of the animal.

PLATE 2

Drawings of various actions of the animal as seen in the film. 1 and 2, protrusion of the web. 3 to 5, a piece of fish touched against the web is seized by the fourth arm. 6, the web is leaving the shell and becoming attached to the glass side of the tank.



Female *Argonauta* in life. (Painted by Miss J. de Vere from a coloured film of the animal).



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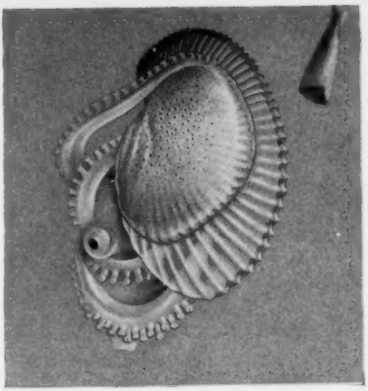

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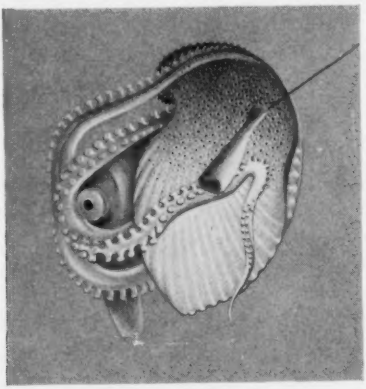

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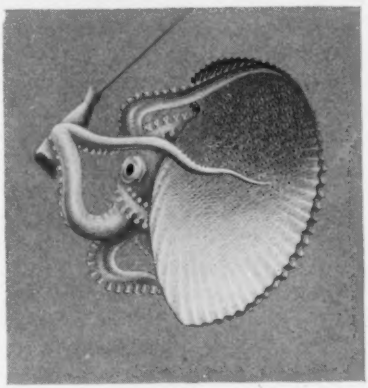

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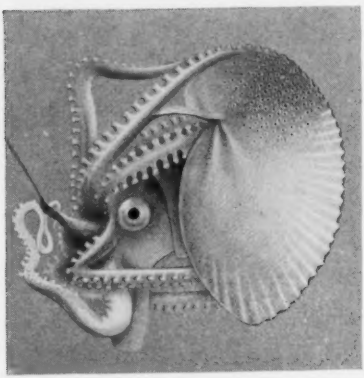

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Female *Argonauta*. Drawings of actions of the animal as seen in the film.

NOTES AND ABSTRACTS

MEETINGS OF THE SOCIETY FOR SCIENTIFIC BUSINESS

12th May 1959

Professor J. Eric Smith, M.A., Sc.D., F.R.S., Vice-President, in the Chair.

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE : APRIL, 1959

By L. Harrison Matthews, M.A., Sc.D., F.R.S.

The registered additions to the Zoological Society's Menagerie in London during the month of April were 195 in number, including some domestic animals. The following are of special interest :—Two Daubenton's bats, *Myotis daubentoni* (Kuhl), new to the collection, presented by the Rt. Hon. The Earl of Cranbrook ; a collection of South-east Asian animals received from F/Lt. E. A. Smith, which includes two slow lorises *Nycticebus coucang*, a Malay tupaia *Tupaia glis ferruginea*, and a Bibron's soft-shelled turtle *Pelochelys bibroni* (Owen) which is new to the collection ; a male tiger purchased as a mate for the female " Susie " received in August 1956 ; a female puma *Felis concolor*, purchased as a mate for the male " Thomas " received in 1951 ; two musk deer *Moschus moschiferus* were received in exchange from the Zoo Centre at Moscow but these, unfortunately did not survive ; two hammer-headed storks *Scopus umbretta* purchased ; and three redshanks *Tringa totanus totanus* presented by Count Leon Lippens. During the same period there were 39 additions to the Menagerie at Whipsnade Park, apart from transfers from London.

The following communications were read and discussed :—

Professor C. Tyler and Dr K. Simkiss. A study of the egg shells of ratite birds. [To be published in the " Proceedings ".]

Dr G. J. Broekhuysen. " Birds of the Vleis " and " Spring in the Cape " (Illustrated by colour films.)

9th June 1959

Dr Errol I. White, F.R.S., in the Chair.

REPORT ON THE ADDITIONS TO THE SOCIETY'S MENAGERIE : MAY 1959

By L. Harrison Matthews, M.A., Sc.D., F.R.S.

The registered additions to the Zoological Society's Menagerie in London during the month of May were 145 in number, including some domestic animals.

The following are of special interest : a pair of Kenya colobus monkeys *Colobus abyssinicus kikuyuensis* Lonnberg, new to the collection. The male was purchased and the female presented by the 4th Battalion of the King's African Rifles ; four Baikal seals *Phoca sibirica* Gmelin, new to the collection, received in exchange ; four northern red-backed voles *Clethrionomys rutilus* Pallas, new to the collection, deposited ; eight Brandt's voles *Microtus brandti* Radde, new to the collection, presented by Dr K. Zimmermann ; a black-tailed hairy tree porcupine *Coendou melanurus* (Wagner), new to the collection, purchased ; a cassowary, sp. inc., presented by F/Lt. E. A. Smith ; a pair of Hartmann's mountain zebras *Equus zebra hartmannae*, purchased ; and two Mississippi saw-back map turtles *Graptemys pseudogeographica kohni* (Baur) new to the collection, presented by Mr John G. Findlater. During the same period there were 49 additions to the Menagerie at Whipsnade Park, apart from transfers from London.

The following communications were read and discussed :—

Mr John Hillaby. Some observations on Cape Hunting Dogs.

Professor G. P. Wells, F.R.S. The geographical distribution of lugworms (Arenicolidae : Polychaeta).

Professor T. Thomson Flynn. The placentation of the Marsupialia.

Dr C. F. Hickling. The Fish Culture Research Station, Malacca.

NOTES ON BRITISH MAMMALS

From

The Scientific Secretaries, Mammal Society of the British Isles.

[Accepted 12th May 1959]

Lesser Horseshoe Bat in West Suffolk

On 18th December 1958, I visited the Glen or Eastgate chalk caves at Bury St. Edmunds, Suffolk, to ring and record bats. In one of the smaller tunnels I found a small bat suspended by its feet from the roof, which was about 1·3 metres (four feet) from the ground. It was torpid and slightly bedewed and upon examination was found to be a female Lesser Horseshoe (*Rhinolophus hipposideros*) which appears to be the first record for Suffolk. It was found again on 9th January 1959 at a distance of about ten metres (thirty feet) from its previous position.

Owing to the extreme rarity of this species in East Anglia it may be of interest to mention previous occurrences in the eastern counties. A specimen found at Girton, Cambridgeshire, is now preserved in alcohol in the University Museum of Zoology, Cambridge. The label is signed " H. Gadow " and dated 1887, though it bears no particulars about the circumstances of capture. Mr Michael Blackmore informs me that he has examined a preserved skin at the Castle Museum, Norwich and that, according to the museum's register, the bat was found at Happisburgh, on the North-east coast of Norfolk, by S. J. M. Davis in June, 1914.

None of the vespertilionid species of bats found in the Bury St. Edmunds caves has been seen hanging from the roof ; they usually hibernate in cracks and holes in the walls, and sometimes even in the floor.

Another interesting find in the same set of caves was a male Pipistrelle (*Pipistrellus pipistrellus*) on 18th November 1958 ; it was subsequently found again thirty-seven days later. Although the Pipistrelle is a common species throughout the British Isles it has seldom been recorded in a cave.

ACKNOWLEDGMENTS

I am very grateful to Mr Michael Blackmore and Dr Owen Gilbert for their help in preparing this note.

REFERENCE

Gilbert, O. & Stebbings, R. (1958). Winter roosts of bats in West Suffolk. *Proc. zool. Soc. Lond.* **131**, 329–333.

R. Stebbings

THE MAMMALS OF THE ISLAND OF SOUTH RONA*

Introduction

South Rona is a small island situated between Skye and the mainland of Wester Ross, approximately five miles from north to south and never

* This investigation was aided by a research grant from the Mammal Society of the British Isles.

exceeding one and a half miles from east to west. Apart from the presence of lighthouse keepers and the periodic visits of the tenant, South Rona is uninhabited, although during the latter half of the last century it supported a population of over 180. The island is of Lewisian gneiss with peat covering. *Juncus* marsh, wet grassland, bracken and birch scrub dominate the lower land ; heather and purple moor-grass are frequent on the higher ground which is never more than 404 ft. above sea level. There is a small, planted, mixed wood south-west of Big Harbour (Fig. 1).

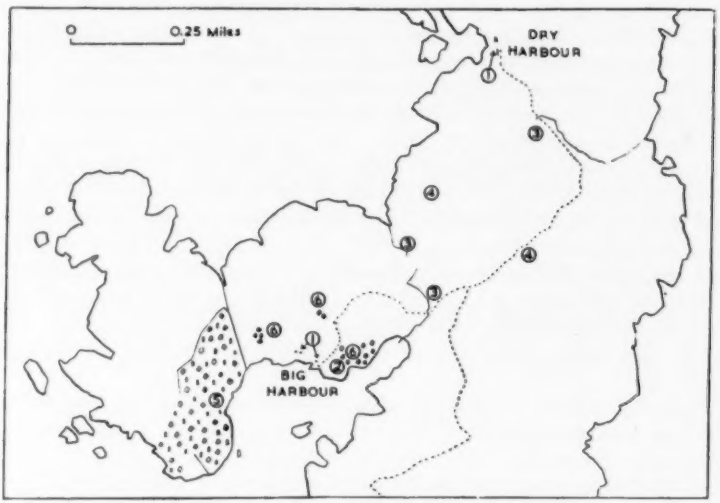


Fig. 1.—Sketch map of the district around Dry Harbour and Big Harbour, South Rona, showing trapping localities (indicated by ringed numerals). Broken lines indicate footpaths and continuous lines indicate walls.

Small mammals

A representative selection of habitats was available for trapping in the vicinity of the former townships of Dry Harbour and Big Harbour. Longworth traps were set for a total of 448 trap-nights between 30th July and 5th August 1958. They were placed in lines with a five yard interval between traps. At first oatmeal alone and later cheese and oatmeal were used as bait. The situation of each habitat where traps were set has been indicated by a ringed numeral on Fig. 1. The trapping results were as follows :—

1. Derelict buildings. With the exception of the Mission House at Dry Harbour these were roofless. Trap nights: thirty-seven. Catch: one, *Apodemus sylvaticus* (L.)* and one, *Sorex araneus castaneus* Jenyns.

* Subspecific identification is withheld pending a revision of the systematics of Hebridean field-mice by one of the authors.

2. *Festuca* grassland with some bracken and *Calluna*. The vegetation was not very dense. Trap nights : twenty-one. Catch ; one, *A. sylvaticus* ; one, *Sorex minutus* L.

3. Alongside stone walls in typical moorland vegetation (*Calluna*, *Erica*, *Molinia*) with bramble, *Dryopteris* and bracken by the most southerly wall. Trap nights : six at wall nearest Dry Harbour, no catch ; thirty-nine at middle wall, no catch ; forty-nine at most southerly wall, three *A. sylvaticus* caught.

4. Moorland with *Calluna*, *Erica*, *Molinia*, *Pteridium*. Trap nights : forty-two. No catch.

5. Mixed wood south-west of Big Harbour. This included Scots pine, birch, rowan, oak, beech, lime, sycamore, Norway spruce and willow. The herb layer included *Primula vulgaris*, *Calluna vulgaris*, *Erica tetralix*, *Pteridium aquilinum*, *Potentilla erecta*, *Corydalis claviculata*, *Blechnum spicant*, *Dryopteris felix-mas*, *Oxalis acetosella*, *Prunella vulgaris*, *Molinia caerulea* and *Galium saxatile*. Mosses were plentiful on the floor of the wood. Traps were set along stone dykes, by a steep bank and in bracken on the edge of the wood. Trap nights : one hundred and twenty. No catch.

6. Birch scrub containing various other species. At Big Harbour bracken was common and in the most easterly of the localities *Calluna* was abundant. Towards the centre of the wood mosses were the only covering to the floor. Trap nights : one hundred and thirty-four. Catch : one, *A. sylvaticus* ; one, *S. minutus* ; four, *S. a. castaneus*.

Small mammals apparently were scarce and of restricted distribution. The mouse was found only along one of the three walls trapped and, like the shrews, was not recorded from the planted wood and the moorland. The absence of small mammals from the wood is surprising, as in other parts of

TABLE 1

Measurements of small mammals from the Island of South Rona

No.	Date	Species	Head and body length (mm.)	Tail length (mm.)	Weight (gms.)	Sex
2803	31. vii. 1958	*A. sylvaticus*	89	87	22	♂
2805	31. vii. 1958	*A. sylvaticus*	94	81*	28	♀
2863	1. viii. 1958	*A. sylvaticus*	87	79*	24	♂
2902	2. viii. 1958	*S. minutus*	61	38	4	♀†
2945	2. viii. 1958	*A. sylvaticus*	61	58	7	♂
3040	3. viii. 1958	*S. araneus*	76	40	6	♂
3073	4. viii. 1958	*S. araneus*	71	45	8	♀
3076	4. viii. 1958	*S. minutus*	55	37	3	♀
3118	4. viii. 1958	*S. araneus*††	78	40	11	♂
3151	4. viii. 1958	*A. sylvaticus*	84	72	20	♀
3165	5. viii. 1958	*S. araneus*	71	45	7	—
3178	5. viii. 1958	*A. sylvaticus*	94	74	20	♀
3204	5. viii. 1958	*S. araneus*	72	40	8	♀

* Tail shortened † One embryo present

†† Fur wet when weighed

north-west Scotland, this type of habitat frequently supports high populations. The absence of voles suggests that Caol Rona, although only half a mile wide, prevents the introduction of *Clethrionomys glareolus erica* (B.–Hamilton and Hinton) from the adjoining Island of Raasay. Alternatively, voles may have failed to enter traps. Mr John Macallum, the present tenant, claimed that a few years ago two small rodents (not mice) entered his house and " appeared to have their tails docked ". Disused rodent runs were present on the side of a steep bank in the mixed wood ; none was seen elsewhere. Measurements of the animals caught are given in the above Table.

Rabbit (*Oryctolagus cuniculus* L.).

Very common, particularly in the Dry Harbour area. Myxomatosis has never reached South Rona.

Otter (*Lutra lutra* (L.))

Common along the coast between Big Harbour and Dry Harbour.

Rat (*Rattus norvegicus* (Erxl.))

Mr John Macleod, a former inhabitant of Rona, informed us that rats were very common on the island up to 1896. The present tenant maintains they are now absent. Their disappearance can probably be associated with man's leaving the island.

Common seal (*Phoca vitulina* L.)

A single individual was seen in the bay at Big Harbour on 31st July 1958. Seals regularly visit rocks at the northernmost tip of the island.

M. J. Delany
W. O. Copland

WOOD MICE AT HIGH ALTITUDE IN SCOTLAND

During trapping for voles near the summit of Cairngorm, Inverness-shire in August 1957, what appeared to be droppings of mice were seen among the stones of the summit cairn (4084 feet). Break-back traps were set, and on the following day (30th August) one contained an adult Wood Mouse (*Apodemus sylvaticus*), unfortunately partly eaten, presumably by shrews. On the same day an adult male was caught in a Longworth trap set on a scree slope on the north side of the hill at an altitude of about 3600 feet. No further trapping was done in the area.

The area around the summit is extremely barren, being almost devoid of vegetation and even of rocks which could provide shelter. However as it is a much-climbed hill, even in winter, there must be a considerable food supply at the summit cairn in the form of scraps (apple cores, etc.) left behind by visitors. On the scree slope strips of vegetation were present, including blaeberry (*Vaccinium myrtillus*) and a scanty growth of the usual alpine species of sedge, rush, grass and moss. The scree was sufficiently stable to provide ample cover in the network of passages and crevices under the boulders. The only other species trapped here were *Microtus agrestis* and *Sorex minutus* (four and one respectively). The ground below the scree was again very

barren and quite unsuitable for any small mammal. The tree limit was about 1500 feet (two and a half miles away) but there was fairly dense heather up to about 2500 feet.

I have been unable to find any published records of *Apodemus* occurring above the tree-line in Scotland. In central Perthshire I have myself trapped an area of established scree at 3000 feet with a much richer flora than on Cairngorm and caught only *Microtus* and *Sorex araneus*. Judging by the numbers of these species caught (over 200) I feel certain that both *Apodemus* and *Clethrionomys* were quite absent. Similarly at Glen Clova, Angus, trapping at 2000 feet, within half a mile of woodland, failed to produce a single *Apodemus* among over 100 animals (*Microtus*, *Clethrionomys* and both species of *Sorex*).

Both specimens obtained were in breeding condition and were exceptionally large, the larger body measurement being exceeded only by one out of a collection of almost 200 specimens from various parts of the Scottish Highlands. The hind feet and tails however are relatively short. The principal measurements are as follows :

	Male	Female
Weight	30 g.	30+g.
Head and body	103 mm.	107 mm.
Tail (from anus)	83	87
Hind foot	22·0	21·4
Ear	17·5	16·0
Condylo-basal length of skull	25·0	24·2

The colour of the pelage is quite normal. The pectoral spot is a small but distinct streak in the male but scarcely visible in the female.

A detailed analysis of the lowland collection, which I intend to carry out shortly, will be necessary before it can be assessed how much, if at all, these individuals differ from typical Scottish *A. sylvaticus*.

G. B. Corbet

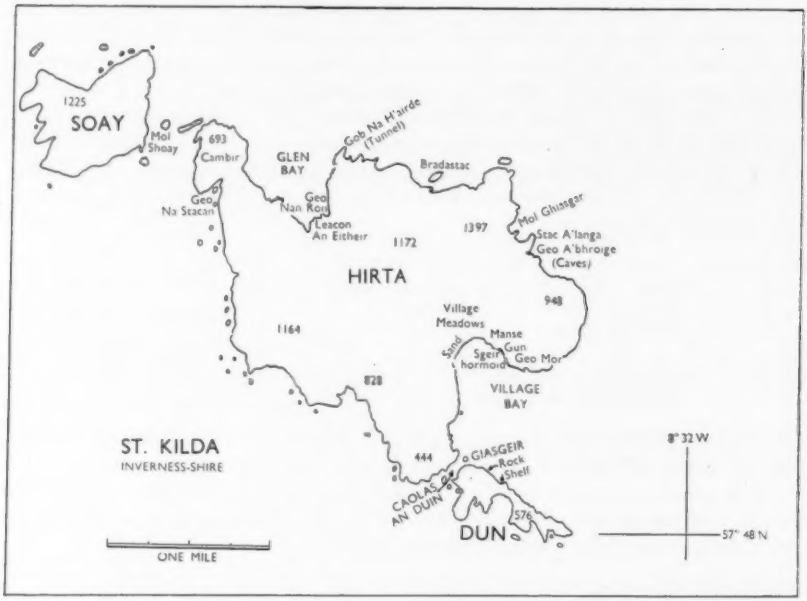
OBSERVATIONS ON THE GREY SEAL AT ST. KILDA IN WINTER

Introduction

In the literature of St. Kilda which goes back to 1697 there is no record of breeding seals. Since the evacuation of the human population in 1930 the possibility of the islands, and particularly the beach and meadows of the village on Hirta, becoming a breeding station of the grey seal *Halichoerus grypus*, has been discussed by Fisher and others. After 1930 no naturalist visited the islands in autumn and winter, and changes in the breeding status of the grey seal have not been recorded. A flight was made over the islands on 30th September 1947 with the express purpose of detecting seal calves, but none was seen (Fisher, 1948). During the winter of 1957–58 I was stationed at St. Kilda as Medical Officer of the R.A.F. Unit, and made the following observations on the grey seal.

Breeding was recorded in Village Bay and Glen Bay from early October to early November. I made an attempt to count the numbers of adults and

calves, but with little success. I was unable to reach most of the breeding grounds, and the animals, which blend with their background, were difficult to count at distance. A very conservative estimate of the number of seal calves born would be: Dun, thirty; Manse, five; Glen Bay, two. Breeding probably took place at Mol Shoay; adults were present, but calves could not be detected from the heights of the Cambir, about half a mile away.



Breeding sites

The seal breeds on flat exposed shelves of rock in the more sheltered bays. They did not breed on rock which exceeded a slope of one in eight, although they would rest on steeper slopes. The calves were sometimes seen among boulders, one being born in such a situation below the old gun near the Manse. Others may have been born on the boulder beach at Mol Shoay, and Dr J. Morton Boyd (*in litt.*) suggests that the recessed boulder beach at Mol Ghiasgar, may also be a breeding site.

Previous writers have suggested that the sandy beach might form the threshold to breeding grounds with wallows along the course of the Amhuinn Mhor, in a situation similar to that found at Shillay, Harris (Hewer, 1956). On no occasion, however, did I see an adult or a calf on the sand, although in the breeding season adults were frequently seen fishing in the surf just off the beach.

Seals were not seen to breed in any of the numerous caves and tunnels, though the only one which I was able to examine was the tunnel at Gob na h'Airde. I made many visits there and despite the fact that there were often

seals present, I was unable to find any evidence of breeding. The sea becomes very rough in periods of heavy swell. Dr Boyd, who visited most of the caves on the lee coasts of Hirta and Boreray (4½ miles to the N.E. of Hirta) in the summer of 1956 states that in only a very few could seals haul out, and none seemed suitable for breeding. A few have boulder beaches in the inner recesses, the one in the left fork of the cave at Geo a'Bhroige being well populated in summer. This cave is protected, but the beach was seen to be completely awash during a visit on a high spring tide.

The rock shelf on the north-east side of Dun, extending for two hundred yards south-east of the entrance of Caoles an Duin, is probably the principal breeding site for seals at St. Kilda. Here there were usually between 100 and 150 adults in October and early November. Other sites were the rock platform below the Manse extending from the quay to Sgeir Thormoid, and the shelf called Leacon an Eitheir in Glen Bay. Calves were also seen on the boulders south of the sand in Village Bay, but they were thought to be strays from Dun. With the exception of Mol Shoay and Mol Ghiasgar all other parts of the coast seem inhospitable to breeding seals.

Breeding season

The first calves were seen on Dun on 6th October. These were in the sea opposite Giasgeir. On 9th October, I saw a calf at Leacon an Eitheir, which, in the light of later experience, I think was about a week old. The last calf for which I have a definite date of birth was born on 3rd November just below the old gun, but on 23 November a week-old calf paid a casual visit to Sgeir Thormoid. Thus the observed breeding season at St. Kilda was from the beginning of October till the middle of November. According to Hewer (1956) and Boyd (1957), the grey seal invades the neighbouring breeding grounds of Shillay and Gasker, Harris, in mid-September, when the first calves are born.

Mortality of calves

I think the mortality of calves is high, and probably of the order of that seen in the colonies on the Pembrokeshire coast (Davies, 1953). After a gale several calves were always missing and the survivors showed signs of their struggle for survival. Some that were swept away succeeded in landing elsewhere in the bay and their mothers were able to find them again. Others were undoubtedly drowned or battered to death by the surf. Survivors were seen to have lacerations on their sides and flippers, and one dead calf which I was able to dissect was found to have died of a dislocated cervical vertebra.

Dr Boyd in his several visits to Dun in summer, 1952–56, did not see any such concentration of seals on the north-east pavement of the island, though a few were usually seen in Caoles an Duin. Dr Boyd and Mr Kenneth Williamson (*in litt.*), the latter having spent the spring, summer and autumn of 1957 on St. Kilda as Warden-Naturalist, say that the main aggregations of seals occur in summer at Mol Shoay, Geo na Stacan and skerries to south, Geos at Leacon an Eitheir and along to Gob na h'Airde, skerries in vicinity at Bradastac, caves near Stac a Langa, Geo Mor, and Coales an Duin. Only small groups of seals were seen in the sea at Boreray. Probably between 200

and 250 seals frequent the archipelago at present, which is comparable to the number estimated by Harrison (1932) in August 1931.

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R. P. Saundby

A SEAL SURVEY OF NORTHERN IRELAND 1956–1957*

Introduction

After a preliminary survey in June 1955 we covered the coast of Northern Ireland during June 1956 and June 1957 in an attempt to identify and count its seal population. Previous information on this subject is summarised by Moffat (1938) but no definite figures are given and it is erroneously stated that *Phoca vitulina* is immeasureably *less* common than *Halichoerus grypus* both in Co. Down and along the greater part of the east coast. No breeding localities are mentioned for *P. vitulina* but Neal and Rankin (1941) report a breeding area in Strangford Lough, and Catford (1930) found a baby seal 2½ feet long on 15th June (obviously a *P. vitulina* pup) at Tyrella, Dundrum Bay, Co. Down.

As *Phoca vitulina* proved to be the dominant seal along this coast, the counts were made in June in order to discover the breeding distribution of this species. Counts of *Halichoerus grypus* were taken at the same time but these are not breeding counts and they only serve to show its comparative rarity.

Daily observations at a breeding colony of *Phoca vitulina* in Shetland (Venables & Venables, 1955, 1957) show that the greatest number of seals haul out (and are therefore most conspicuous) at low water on a calm day without onshore swell, and our counts in Northern Ireland were mainly done under such conditions. It was rarely possible to count an area more than once but where repeat counts were made the highest figure has been given. Even so, the counts given below *do not represent the maximum number of seals in the area*. For one thing it was impossible to keep a check on human disturbance which is always an important factor on such occasions. Also there was a certain amount of " dead ground " ; perhaps the most important being among the shallow " pladdies " (too shallow for our boat) towards the north end of Strangford Lough. The main coastal counts were made from the shore, and for off-lying islands we made use of boats, but for a few inaccessible

* This survey was aided by a research grant from the Mammal Society of the British Isles.

skerries we had to rely on long shots with the telescope. In long shots the pup seals are particularly difficult to see. Nevertheless our results give a fair indication of the size and make-up of the June population round these coasts and map the exact distribution of the *Phoca vitulina* breeding colonies.

These counts apply only to seals actually seen by us in 1956 and 1957.

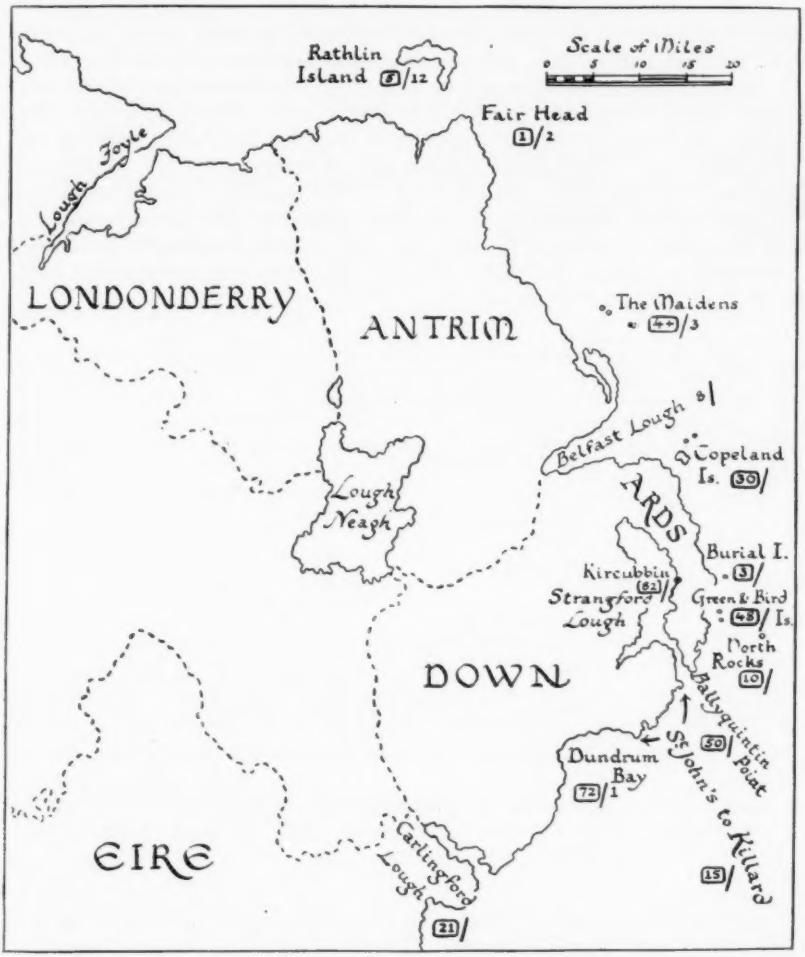

Fig. 1.—Seal distribution in Northern Ireland. Figures on the left of the diagonals represent the number of *P. vitulina* seen : on the right the number of *H. grypus*. Enclosed figures indicate a pupping area.

Though we summarise the information given us by local fishermen concerning occasional seals seen here and there, we do not include these in our totals. One section of coast, Killard Point to Minerstown, Co. Down, remained uncounted owing to difficulties of time and transport. This was kindly counted by C. D. Deane of the Belfast Museum in June 1958 and his figures have been incorporated.

The pupping season in Northern Ireland

Pupping with *Phoca vitulina* in Shetland extends from about 14th June to 5th July (Venables & Venables, 1955). For the Wash, East Anglia, Professor R. J. Harrison tells us that, though he found an early pup on 27th May 1957, the normal pupping season is 6th to 25th June with the majority born 19th to 23rd June. Pupping in Northern Ireland begins earlier. Two fishermen (Co. Down and Co. Antrim) told us that first pups can regularly be seen at the end of May, and J. Kirkpatrick found a pup (probably newly born) on Burial Island on 19th May 1957. Neal & Rankin (1941) caught a pup on 20th June estimated at two to three days old, with its umbilical cord still intact, so pupping lasts for at least a month. We saw a well-grown and independent (i.e. unaccompanied) pup going out to sea through the narrows of Strangford Lough on 1st July 1957. This pup would have been about five weeks old.

Numbers of seals

County Down

Warrenpoint to Dundrum 23/6/57
21 *P. vitulina* and 1 pup (Carlingford Lough)

Dundrum to Craigalea 19/6/56
27 *P. vitulina* and 1 *H. grypus*
Ringsallin to St. John's Point 25/6/58
45 *P. vitulina* and 5 pups
} (Dundrum Bay)

St. John's Point to Killard Point 25/6/58
15 *P. vitulina* and 1 pup

Entrance to Strangford Lough 20/6/56
50 *P. vitulina* and 2+ pups (Ballyquintin Point)
(Seal shooting here in August 1957)

Strangford Lough 17/6/56
(Rocks 1½ miles from Kircubbin. Some areas of " dead ground ")
82 *P. vitulina* and 4 pups
(Most of this area is preserved against shooting)

Ards Peninsula 14–21/6/56
North Rocks 8–10 *P. vitulina* (pupping locality)
Bird and Green Islands 48 *P. vitulina* and 1 pup
Burial Island 3 *P. vitulina* and 1 pup

Belfast Lough 13/7/57
8 *P. vitulina*
(Hauling out terrain near mussel beds on south side)

Copeland Islands 22/6/56
Ca. 30 *P. vitulina* (pupping locality)

Total for Co. Down
337–339 *P. vitulina* and 15+ pups
1 *H. grypus*

County Antrim

MAINLAND COAST 24–28/6/57

Much commercial salmon netting and consequent seal shooting. Very few areas of shore suitable for pupping *P. vitulina* except for parts of the Giant's Causeway (where there must be a good deal of tourist disturbance).

Fair Head 1 *P. vitulina* and 1 *pup.* 2 *H. grypus*

No other seals seen but fishermen say they see an " occasional " seal at any season, especially near the Giant's Causeway, and we had reports of two early summer pups (therefore presumably *P. vitulina*) over recent years at White Park Bay (drowned in a salmon net) and Larne Lough (shot).

THE MAIDENS' GROUP 25/6/57

4 *P. vitulina* and 1 pup. 3 *H. grypus*

6+ *unidentified seals*

(Seal shooting by fishermen taking place, so an unsatisfactory minimum count)

RATHLIN ISLAND 15–22/6/57

5 *P. vitulina* and 1 pup. 12 *H. grypus*. Frank McCurdy of Rathlin told us in 1957 that he had seen a Grey Seal pup in a sea-cave there during a " recent autumn ".

Total for Co. Antrim

10 *P. vitulina* and 3 pups
17 *H. grypus*
6+ unidentified seals

County Derry

A much shorter coastline with little suitable terrain for pupping *P. vitulina*. A great deal of commercial salmon netting. The fishermen see an occasional " big seal " in Lough Foyle and " brown seal " in the estuary of the Foyle River. They suggested that these seals came round from Donegal (Malin Head and Lough Swilly) and said that they had never seen a pup in Derry. The Foyle Fisheries Commission offers a 15s. head reward but only about two were claimed last year (1956).

28–29/6/57. We saw no seals at all on the coast of Co. Derry or in Lough Foyle.

Total for Northern Ireland

Adult *Phoca vitulina*	347–349
Pup *Phoca vitulina*	18+
Adult *Halichoerus grypus*	18
Unidentified seals	6+

These surprisingly low numbers are due, in great part, to artificial control by fishermen. Along the coasts of Antrim and Derry the lucrative salmon netting season coincides with the *Phoca vitulina* pupping period when the seals are most vulnerable: the young pups are novices in the water and the mothers are loth to desert them.

Thus the main *Phoca vitulina* population is centred in Co. Down, pupping particularly in Dundrum Bay and in the sheltered waters of Strangford and Carlingford Loughs, which suffer relatively little disturbance.

Acknowledgments

Among many helpers we particularly wish to thank C. Douglas Deane of the Belfast Museum and Doris Deane of Knock for their very considerable help and hospitality, J. Kirk of Ballynahinch for help and information, and the Mammal Society of the British Isles for a monetary grant towards boat hires.

Summary

In June 1956 and June 1957 an attempt was made to identify and count the seal population of Northern Ireland. The whole coast was covered but the figures obtained are *strictly minimal.*

Phoca vitulina. 347+ adults and 18+ pups were found. Seal shooting by commercial salmon-netters helps to restrict numbers, especially in Co. Antrim and Co. Derry, and the main population is centred in Co. Down.

Pupping with *Phoca vitulina* begins during the end of May : about a week earlier than in the Wash (East Anglia) and about a fortnight earlier than in Shetland. A map is given showing the pupping localities.

Halichoerus grypus. With the exception of one found hauled out with some *vitulina* in Dundrum Bay, Co. Down, all the rest (17) were on the Antrim coast (Fair Head, Rathlin and The Maidens). A pup is locally reported from Rathlin Island.

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U. M. Venables and L. S. V. Venables

SUPERNUMERARY TEETH IN THE BADGER

The examination of the skull of a young adult male badger (*Meles meles*), which was run over near Selsdon in Surrey and is now at the Chelsea College of Science and Technology, revealed the presence of supernumerary teeth.

The normal dentition of the badger is $\frac{3\ 1\ 3\ 1}{3\ 1\ 3\ 2}$, whereas that of the specimen being considered was $\frac{3\ 1\ 4\ 2}{3\ 1\ 4\ 2}$, an increase in the number of premolars and molars. The difference is due, in part, to the presence in each jaw of the vestigial premolars, which are a not uncommon character. The extra molar in the upper jaw is the result of the replacement of the large molar by two separate and smaller teeth, each having three roots. This has produced an extension of the maxilla posteriorly, into the orbit. The last molar of the lower jaw is considerably enlarged, possibly correlated with the increased length of the upper jaw. The first molar is, however, smaller than usual. The left incisor of the upper jaw was diseased and the socket considerably shallower than normal. The other teeth appeared to be normal.

P. J. Fullagar
T. H. Rogers
D. Mansfield

NOTICE

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LIST OF CONTENTS

Vol. 133

Part 3 (pp. 337–494)

Page

Adamson, L., Harrison, R. G. and Bayley, Iris
The development of the whistling frog *Eleutherodactylus martinicensis* of Barbados. (4 plates) 453

Alexander, Anne J.
A note on the evolution of stridulation within the Family Scorpionidae. (1 plate and 2 figures) 391

Atkins, D.
The development of the pleopods in the young crab stages of *Pinnotheres* (Crustacea). (13 figures) 435

Austin, A. P. *See* Ryland, J. S.

Bayley, Iris. See Adamson, L.

Harrison, R. G. See Adamson, L.

Kerr, T.
Development and structure of some actinopterygian and urodele teeth. (2 plates and 2 figures) 401

Ryland, J. S. and Austin, A. P.
Three species of Kamptozoa new to Britain. (1 plate and 3 figures) 423

Schultz, Adolph H.
Age changes and variability in the skulls and teeth of the Central American monkeys *Alouatta*, *Cebus* and *Ateles*. (3 plates and 7 figures) 337

Young, J. Z.
Observations on *Argonauta* and especially its method of feeding. (2 plates and 2 figures) 471

Notes and Abstracts :
Report on the additions to the Society's Menagerie, April and May 1959 p. 481 by L. Harrison Matthews ; Notes on British Mammals :— Lesser horseshoe bat in West Suffolk by R. Stebbings p. 483 ; The mammals of the island of South Rona by M. J. Delany and W. O. Copland p. 483 ; Wood mice at high altitude in Scotland by G. B. Corbet p. 486 ; Observations on the grey seal at St. Kilda in winter by R. P. Saundby p. 487 ; A seal survey of Northern Ireland 1956–57 by U. M. and L. S. V. Venables p. 490 ; Supernumerary teeth in the badger by P. J. Fullagar, T. H. Rogers and D. Mansfield p. 494.

NOTICE

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